

The Origins of Modern Humans

The Origins of Modern Humans

Biology Reconsidered

Edited by

Fred H. Smith and James C. M. Ahern

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In Memory of Frank Spencer (1941–1999)

A Kent Limey in the Court of Queens—and Windsor and Ann Arbor
(with apologies to Mark Twain)

Contents

(All papers in this volume have been peer reviewed.)

<i>Contributors</i>	ix
Introduction: Thoughts on Modern Human Origins: From 1984 to 2012 <i>Fred H. Smith and James C. M. Ahern</i>	xi
1 Africa: The Cradle of Modern People <i>Osbjorn M. Pearson</i>	1
2 Crossroads of the Old World: Late Hominin Evolution in Western Asia <i>Robert G. Franciscus and Trenton W. Holliday</i>	45
3 A River Runs through It: Modern Human Origins in East Asia <i>Karen R. Rosenberg and Xinzhi Wu</i>	89
4 Perspectives on the Origins of Modern Australians <i>Arthur C. Durband and Michael C. Westaway</i>	123
5 Modern Human Origins in Central Europe <i>James C. M. Ahern, Ivor Janković, Jean-Luc Voisin, and Fred H. Smith</i>	151
6 The Makers of the Early Upper Paleolithic in Western Eurasia <i>Jean-Jacques Hublin</i>	223
7 Neandertal Craniofacial Growth and Development and Its Relevance for Modern Human Origins <i>Frank L'Engle Williams</i>	253
8 Energetics and the Origin of Modern Humans <i>Andrew W. Froehle, Todd R. Yokley, and Steven E. Churchill</i>	285
9 Understanding Human Cranial Variation in Light of Modern Human Origins <i>John H. Relethford</i>	321
10 The Relevance of Archaic Genomes to Modern Human Origins <i>John Hawks and Zach Throckmorton</i>	339

11 The Process of Modern Human Origins: The Evolutionary and Demographic Changes Giving Rise to Modern Humans	355
<i>Rachel Caspari and Milford H. Wolpoff</i>	
12 The Paleobiology of Modern Human Emergence	393
<i>Erik Trinkaus</i>	
<i>Index</i>	435

The color plate section can be found between pages 242 and 243.

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Introduction: Thoughts on Modern Human Origins: From 1984 to 2012

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Origins of Modern Humans (1984)

A Perspective from a Student (JCMA)

In the late 1980s, I went off to college interested in a handful of possible futures but certain of none. A moment of clarity came in a “theory and method in physical anthropology” class when the topic of the week, and of one of my papers, turned toward modern human origins. This had become the hot topic of paleoanthropology by the late 1980s and had largely eclipsed the field’s obsession with hominin origins. As I delved into its literature for the first time, I encountered a single book that not only was a wealth of information for the paper that I needed to write but also the work that had been instrumental in changing the focus of paleoanthropology. This book, Smith and Spencer’s *The Origins of Modern Humans: A World Survey of the Fossil Evidence* (1984), was a weighty tome that I felt as I carried it around with me for the rest of the semester and well after I had turned in my first paper on modern human origins. Other books on modern human origins had come out by the late 1980s and all had their own strengths. However, what set *Origins* apart, aside from being the first, was its detailed fossil descriptions and decidedly new theoretical explanations combined with comprehensive geographical coverage. Many of the book’s chapters went on to become core readings for any student of physical anthropology, and the book as a whole became essential for all paleoanthropologists. *Origins* transformed me and many others from undeclared college students into anthropology majors determined to become paleoanthropologists.

A Perspective from an Editor (FHS)

My late friend and colleague, Frank Spencer, and I conceived the idea for a volume on the fossil record relevant to the origin(s) of modern humans in the early 1980s. Because paleoanthropology during the 1970s and early 1980s had focused primarily on earlier stages of human evolutionary history, we felt that a volume presenting various perspectives on later human evolution would be a timely and valuable contribution. Furthermore, Frank and I believed those perspectives should be presented within the context of detailed regional analyses of the fossil evidence, so we conceived a series of papers that would take regional, as well as theoretically varied, approaches. We also felt it was important to demonstrate the continuation of some of the same evolutionary trends involved in modern human origins after the appearance of modern people. Thus the *Origins of Modern Humans: A World Survey of the Fossil Evidence* (Smith and Spencer, 1984) covered both late Pleistocene and aspects of early Holocene human skeletal evolution.

In *Origins of Modern Humans*, chapters covered four broadly defined geographical regions: Africa, Western Asia (including the western areas of the then Soviet Union), East Asia, and Europe. Europe was split into Western and Central Europe because of the wealth of the European fossil record and to ensure the Central European evidence was not eclipsed by the tendency to focus on Western Europe, as had been the case through the middle decades of the twentieth century (see, e.g., Boule and Vallois, 1957). This European split also provided for more diversity of perspective as the Western European chapter was written from a decidedly “replacement” explanation for the appearance of modern people in Europe (Stringer et al., 1984), while the Central European chapter took a view of significant continuity between Neandertals and early modern Europeans (Smith, 1984). In addition, Wolpoff, Wu, and Thorne provided the first comprehensive explanation of multiregional evolution (Wolpoff et al., 1984), and Bräuer (1984) presented the most complete initial discussion of his “Afro-European Sapiens Hypothesis.” Wolpoff and colleagues’ discussion centered on the fossil material from East Asia and Australasia, areas that strongly influenced Weidenreich’s trellis model of later human evolution, in many ways the intellectual precursor to multiregional evolution. Although not Bräuer’s first publication with the Afro-European Sapiens theme, it was his earliest comprehensive statement on the African fossil record’s demonstration of the origin of modern humans on that continent. Rightmire (1984) also stressed the importance of Africa, particularly the likely early appearance of modern humans there. While the Western European chapter supported a replacement of Neandertals by incoming moderns in Europe, Stringer and colleagues, like Bräuer, also suggested the possibility of some introgression. However, Stringer and colleagues were more equivocal regarding an African origin for modern humans. They state that “the place of origin of the first hominids with a total morphological pattern matching that of recent humans is not identifiable from the present fossil record” (Stringer et al., 1984: 121). The basis of this statement was not a lack of relevant fossils but the problem of dating the late Pleistocene human fossil record, particularly outside Europe. Dating uncertainties recur in the 1984 papers dealing with initial modern human origins in all regions.

Both the Central Europe and Western Asia (Trinkaus, 1984) chapters supported models that involved considerable continuity from Neandertals to early modern people in these respective regions and more generally from archaic to modern humans throughout the Old World. Both chapters also evoke cultural/environmental adaptation as major factors influencing the timing and pattern of modern human emergence. In 1984, these ideas could be encompassed under a fundamentally multiregional model as opposed to a single-origin, more replacement-focused model. Thus the 1984 volume played a fundamental role in defining the dichotomy of perspective that dominated the debate on modern human origins throughout the remainder of the twentieth century: multiregional evolution versus a single regional origin model in which the spread of modern humans from the source region resulted in replacement of the archaic peoples indigenous to other regions. Focus on this dichotomy continues into the twenty-first century and has been clearly reflected in subsequent edited volumes dealing broadly with modern human origins (Mellars and Stringer, 1989; Trinkaus, 1989; Hublin and Tillier, 1991; Bräuer and Smith, 1992; Aitken et al., 1993; Nitecki and Nitecki, 1994; Clark and Willermet, 1997), as well as those more focused on Neandertals and their role in later human evolution (Conard, 2006; Harvati and Harrison, 2006; Condemi and Weniger, 2011).

New Data and Directions on the Heels of 1984

In the mid-1980s, it seemed important to specify what was needed to falsify one or the other of these dichotomous models. So in 1985, Smith established three criteria that should be met in order to demonstrate replacement of all archaic humans throughout the Old World by

modern humans that emerged in a single region. First, modern humans would have to be found in a single region demonstrably earlier than in other regions. Second, modern humans must be shown to overlap with archaic peoples in some places. And third, there should be some demonstration of a cause for the expansion of modern humans from their natal area to other regions. In the early 1980s, it could still be convincingly argued that modern humans appeared in various areas of the Old World at basically the same time, approximately between 35,000 and 45,000 years ago. Although there were certainly claims for an earlier presence of moderns in both West Asia and Africa, there was no compelling evidence that moderns were significantly earlier in any one specific region, nor was there a strong indication of the movement of modern morphology from any supposed region of origin into other areas. Similarly, if moderns migrated into other regions they should have temporally overlapped with indigenous populations and left, at least in some regions, evidence of that overlap. At that time, no such unequivocal evidence of such overlap was available, nor was there a clear demonstration of the geographic spread of modern people from a single region. Based on these factors, multiregional evolution could not be falsified and actually, in the opinions of many, provided the most parsimonious explanation for modern human origins throughout the Old World.

Just after the mid-1980s, evidence emerged that related directly to these criteria. H. Valladas and colleagues published three papers on the application of thermoluminescence (TL) dating to the Western Eurasian late Pleistocene fossil human record. This work was significant for two reasons. First, it demonstrated, for the first time, use of a reliable technique capable of providing chronometric age estimates during the critical period for modern human origins, between circa 200,000 and 40,000 years ago, albeit not directly on the fossils. Second, results from TL estimates provided convincing support for the early appearance (92 ± 5 kya—or thousand years ago) of modern humans at Qafzeh in the Near East (Valladas et al., 1988) and more recent ages for Neandertals in both Europe (Le Moustier @ 40.3 ± 2.6 kya; Valladas et al., 1986) and in the Near East (Kebara @ 61.6 ± 3.6 kya; Valladas et al., 1987). Soon TL was joined by electron spin resonance, which could provide chronometric dates, often directly on human fossils that broadly supported the pattern emerging from TL dating (Grün and Stringer, 1991). Other chronometric dating techniques also began to have a greater impact on understanding this time period, including accelerator mass spectrometry (AMS) radiocarbon and other aspects of uranium-series dating (see Aitken et al., 1993).

Another line of evidence started to gain attention at roughly the same time. In 1982, a study of over a hundred nuclear genes by Nei and Roychoudhury suggested that modern Eurasia populations split from Africans at 110 ± 34 kya, supporting earlier interpretations (see Howells, 1976). While the large error raised questions about the accuracy of some of these earlier genetic estimates, additional evidence emerged with the initial studies by Cann and colleagues (1987) on worldwide modern human mitochondrial (mt) DNA distribution. This study indicated that all modern human mtDNA originated in Africa and that the first modern Eurasian population diverged from Africans between 90 kya and 180 kya. Although this interpretation of the mtDNA data had its critics, the fact that it was supported by other genetic studies proved very compelling, as did further research on the mt genome that answered many of the initial criticisms (see reviews in Relethford, 2001, and Cartmill and Smith, 2009). Joining this new dating and genetic evidence with morphological evidence presented in the *Origins of Modern Humans* (particularly the works by Bräuer and Rightmire) and other sources, Stringer and Andrews (1988) formulated the Recent African Origin model, which explained modern humans as the result of a speciation event in Africa and as the instrument of archaic human replacement in Eurasia. This model, or very similar variants of it, became almost immediately the most widely embraced explanation for the origin (not origins) of modern people.

By the late 1980s, the classical version of the multiregional model seemed unlikely to be the most parsimonious explanation for modern human origins. This perception was supported by both the morphological and genetic evidence available, but it was primarily influenced by the emerging pattern of chronology indicating earlier appearance of modern humans outside than within Eurasia (except for the Levant). This suggested there likely was a specific region of origin for modern human biology. However, there were reasons to reject the complete replacement of Neandertals and other archaic people by a new species of modern humans. For example, the late Neandertal remains from Vindija suggested that later Neandertals showed a morphological pattern demonstrating integrated change in the direction of the modern human morphological pattern (Smith, 1984). Furthermore, early moderns in Central Europe possessed anatomical features that were best explained as the result of Neandertal contribution to their ancestry. Prior to the dating “revolution” of the later 1980s, these observations could be interpreted as indicating that Neandertals were evolving in the direction of modern Europeans within the multiregional perspective of regionally based, interconnected lineages. But even in 1984 the current volume’s senior editor wrote: “in my estimation the increasing evidence for the early appearance of modern *H. sapiens* elsewhere strengthens the possibility that unidirectional gene flow into Europe . . . played a significant role in the emergence of modern Europeans. However, even if gene flow’s role were significant, the nature of morphological continuity demonstrates that the Neandertal gene pool was a major contributor to that of early modern Europeans” (Smith, 1984: 196).

After 1984, reconsideration of the Central European Neandertal and early modern morphological evidence suggested that the amount of Neandertal contribution generally had been overestimated, including Smith’s 1984 assessment. For instance, it became more evident that continuity was primarily reflected in morphological details, not in overall anatomical form. The combination of this with the dating evidence led to the formulation of the assimilation model for modern human origins by the end of the 1980s (Smith et al., 1989), although aspects of it were emerging earlier (see Smith, 1985; Trinkaus and Smith, 1985). This model differed from the multiregional evolution of the late 1980s and early 1990s in that it supported the likelihood of a specific region of origin for modern human biology as a complex and suggested Southern Africa as likely, but not definitely, that region. Like multiregional evolution, however, assimilation rejected the occurrence of a speciation event associated with that origin and argued that Eurasian regional populations of archaic humans were not totally replaced.

One problem relating to an African origin for modern humans in the 1980s was the uncertainty of the dating of sites like Omo-Kibish KHS and Border Cave (Smith et al., 1989), both of which were claimed to show modern humans in Southern Africa prior to 100 kya. The morphologically modern Omo-Kibish I specimen (from Ethiopia) was dated to ~130 ka on the basis of uranium-thorium dating of mollusk shell (Butzer, 1969), but this was considered problematic because of inherent uncertainties in applying the technique to shell. The morphologically modern Border Cave crania and mandibles were of uncertain context, except for the Border Cave 3 infant and Border Cave 5 mandible. Taking a cautious approach to both of these sites in 1989 was certainly reasonable, but things have changed. New research has led to the bracketing of the Omo-Kibish I skeleton between 172 kya and 196 kya (McDougall et al., 2005, 2008), demonstrating that modern human anatomy was established in Africa at an early date. Subsequently this has been enforced by the discoveries of early modern specimens at the site of Herto, also in Ethiopia, securely bracketed between 154 kya and 160 kya (White et al., 2003). Added to the evidence for an early transition between archaic and modern humans in Africa (see Pearson, this volume; Bräuer, 2008; Cartmill and Smith, 2009), the fossil evidence from Omo-Kibish and Herto establishes that modern human morphology does indeed initially appear in Africa, perhaps specifically in

East Africa. Thus, the criterion of establishing an area of origin for modern humans, as previously discussed, has been met (at least in light of our current knowledge).

Better dating and new discoveries also have improved our picture of the appearance of modern people in much of Eurasia. The robust but fundamentally modern sample from the sites of Qafzeh and Skhul in Israel likely dates between 81 kya and 119 kya (see Cartmill and Smith, 2009). Unfortunately there have been no new early modern specimens from this pivotal region since the 1984 review. The same is not true for further east in Asia and in Australasia, where important finds have been made in China since 1984 (see Rosenberg and Wu, and Durband and Westaway, this volume). Also in Europe, especially Central Europe, there has been significant change in the evidence for early modern people (Aherne and colleagues, this volume). Overall, the pattern of modern human appearance in Eurasia is commensurate with the spread of modern human morphology as a unit from Africa to the Near East and then to other portions of the Old World, likely reaching Europe rather late but perhaps not as late as previously thought. Recent new dates and analyses on specimens from Italy and England possibly push the earliest skeletal evidence for modern humans in Europe to as early as 45,000 years ago (Benazzi et al., 2011; Higham et al., 2011). This pattern is yet another indication that modern human biology emerged and spread fundamentally as a unit (but see Rosenberg and Wu, this volume).

The evidence available today relative to the two other criteria established in 1985 is more equivocal. Temporal overlap of Neandertals and early modern people in the Near East and Europe is highly likely, but in the rest of Asia it is virtually impossible to establish. In the Near East, many scholars argue that there was not extensive overlap but rather a shifting boundary between modern people migrating up from Africa and Neandertals pushed south by European glaciations (see Franciscus and Holliday, this volume). In Europe, evidence for actual temporal overlap is convincing, but for both regions morphological evidence for actual biological introgression is intensely debated, as the various papers in this volume attest.

The third criterion deals with why moderns would have moved out of Africa, especially into an area where well-adapted hominins, the Neandertals, would have to be contended with. The most likely culprits that could provide such a motivation would be population pressure, climate/environmental change, or some combination of both. Past population size is painfully difficult to measure, particularly from a paleontological or archaeological perspective. Based on site density, Hassan (1981) calculated that people associated with Upper Paleolithic/Late Stone Age technology were some three times more common on the landscape than those associated with Middle Paleolithic/Middle Stone Age, some of whom were anatomically modern as well. Additionally, genetic studies indicate that effective population size in Africa was larger than in Eurasia throughout the Pleistocene (Relethford, 2001) and that effective population size was significantly smaller in Neandertals than moderns (Briggs et al., 2009). Still it seems unlikely that these differences were great enough to support an argument of simple population pressure as the cause for modern human expansion out of Africa. From another perspective, these data indicating smaller population sizes for Neandertals, recently supported by additional analysis of Mousterian and early Upper Paleolithic sites in Southwestern France (Mellars and French, 2011) suggest that Neandertals were relatively rare on the landscape. This was likely a significant factor in their seemingly rapid “disappearance” in the face of increasing density of incoming modern human populations (Smith, 2011).

Climatic reconstructions during the Middle and Late Pleistocene have long depended on the use of Marine Oxygen Isotope Stages (or MIS) (see reviews in Cartmill and Smith, 2009, and Klein, 2009) and more recently lake cores from the Rift Valley (Scholz et al., 2007; Cohen et al., 2007). Anatomically modern humans first emerged in East Africa between 196 and 154 kya (MIS 6) and reached the Near East to Israel minimally by 81 kya and perhaps

as early as 119 kya, within MIS 5. MIS 6 was an elongated cold period extending from 186 kya to 127 kya during which temperatures were significantly colder than today. However, new research based on lake sediment cores from Lake Malawi and Lake Tanganyika in the East African Rift Valley (Scholz et al., 2007) suggests the truly marked times of extreme aridity were between 135 kya and 75 kya and that climate was quite variable during this span. More arid conditions in Eastern Africa could have put pressure on populations to roam farther in search of resources, including movement through Northeastern Africa toward the Near East. However, the MIS provide a different picture on a broader scale. By MIS 5e, beginning around 130 kya, the world was getting warmer and wetter during the last major interglacial. The Near East perhaps became even more attractive for African migrants, and even North Africa areas that are today desert yield evidence of wetter, lush conditions during parts of MIS 5 (Castañeda et al., 2009). Thus the combination of potentially dryer conditions in Eastern Africa and possible more attractive conditions in North Africa and the circum-Mediterranean region might explain the modern human migration to the North that ultimately led to further spread into Eurasia as a whole.

It is certainly possible, indeed attractive, to explain the initial anatomically modern human movements out of Africa as the result of interplay between the pressures of arid conditions and population sizes in Africa. However, these might not have been of the magnitude to push people toward an out-of-Africa migration pattern. The fact is we just are not certain why the pattern of migration began and continued. The arguments for overlap of archaic and early modern people in the Near East and Europe, and the potential impact of climate and population pressure, are certainly intriguing. A recent discussion of the impact of refugia also adds insights to the role of climate in the process of modern human origins and the disappearance of Neandertal populations (Stewart and Stringer, 2012). Overall though, the second and third criteria established in 1985 are less clearly supported by the available evidence today as the first criterion is. There is still more work to be done in these areas.

History

Frank Spencer's contribution to the original *Origins of Modern Humans* was an assessment of the history of the study of modern human origins (Spencer, 1984). In his chapter Frank detailed the impact of Piltdown and pre-sapiens perspectives, as well as the changing view of Neandertals from the late nineteenth century, through Boule's influential work—particularly focusing on the analysis of the La Chapelle-aux-Saints skeleton. He also discussed the impact of Hrdlička's "Neanderthal Phase of Man," and the contributions of Schwalbe, Keith, Weidenreich, and Vallois. Frank's assessment of this history became easily the most cited paper on the pre-1980s history of later human evolution. This stems from the fact that few previous articles managed to take such a broad view yet still provided the detail necessary to be useful to other researchers. The issues Frank elucidated in 1984 were expanded in his seminal two-volume work, *History of Physical Anthropology: An Encyclopedia* (Spencer, 1997). In that volume, numerous entries deal with modern human origins, and later works have helped to connect Frank's perspectives with events and discoveries since 1984 (Smith, 2002; Delisle, 2007; Cartmill and Smith, 2009). Because of these recent updates to the history of later human evolution, we felt an independent chapter devoted to history was not as critical as it was in 1984.

Of course, another factor was that there was no Frank Spencer to contribute such a chapter. Frank's untimely passing in 1999 robbed us of a uniquely informed historical perspective on our discipline and left a void yet to be fully filled. As an alternative to an independent history chapter, the contributors to this current volume were asked to include historical perspectives where appropriate, and most of them have provided informative

historical insights in their contributions. Still, for those of us who counted him as a trusted colleague and friend, Frank's words are sorely missed. For all that Frank did and was, we are proud to dedicate this volume to his memory.

Origins of Modern Humans (2012)

In deciding on coverage of Africa, Asia, and Australia for the current volume, we (Smith and Ahern) concluded that the regional approach of the 1984 book was still appropriate, except that we decided to separate East Asia and Australasia. This was based on the fact that more evidence has accumulated in East Asia, as well as the recognition that these regions were different enough from each other to warrant separate considerations. We decided further that there was no need to repeat basic description for all of the fossil material discussed in 1984. Rather, we asked the authors of regional chapters to focus on new fossil discoveries, using older material when relevant. We also asked contributors to place their region in a broader context of modern human origins, including commenting on history, genetics, patterns in other regions, and any other factors they felt were appropriate. Furthermore, we maintained the variation of perspective in these regional chapters that characterized the 1984 volume. In the current volume, Osbjorn Pearson discusses the African fossil material and presents the strong paleontological indicators of an early presence of modern people on that continent, as well as considerations of potential climatic reasons for the spread of modern populations out of Africa and some useful insights on the issue of speciation in later human evolution. Robert Franciscus and Trenton Holliday focus on the complexities of the fossil record in Western and Central Asia and European Russia. They conclude that, despite the potential for temporal overlap, Neandertals and early modern humans remained separate in Western Asia. The mainland East Asian record is considered by Karen Rosenberg and Xinzhi Wu. They note that because East Asia occupies one of the extreme peripheries of human habitation during the Pleistocene, it is an ideal place to test models about human origins. Current consideration of what is a richer, better dated fossil and archaeological record, as well as new genetic data, is consistent with Weidenreich's original impressions emphasizing continuity and varying levels of gene flow with western parts of the Old World. Arthur Durband and Michael Westaway provide an overview of modern human origins in Australasia. Their perspective differs radically from that offered for Australasia in 1984, which touted Australasia as a region strongly demonstrating regional continuity (Wolpoff et al., 1984). Durband and Westaway argue there is no evidence for any morphological continuity between archaic Australasians (e.g. Ngandong) and modern people in island Southeast Asia or greater Australia.

In Europe, we also maintained the geographic split between Central and Western Europe, although we recognize there will be some overlap of coverage around the Rhine River. Jean-Jacques Hublin tackled the issue of cultural and biological identity of makers of the early Upper Paleolithic in Europe, with a focus on Western Europe (including Germany). He asserts that there is little compelling evidence for either biological or cultural continuity between Neandertals and early modern human populations. Central Europe is discussed by Ivor Janković, Jean-Luc Voisin, and us. Although we maintain that there was some continuity between late Neandertals and early modern people in this part of Europe, the nature and extent of that continuity is recognized to be different from that proposed by Smith in 1984. There are also significant changes to the fossil record in Central Europe since 1984, particularly with regard to early modern specimens.

In addition to the regional papers, we wanted to include other biological parameters that have become much more significant to the understanding of modern human origins than

was the case in 1984. Recent years have witnessed a great deal of work on Neandertal ontogeny and developmental biology, most of which has identified significant differences between Neandertals, the only archaic hominin for which such data can be reliably generated, and modern people. Frank L'Engle Williams reviews the craniodental evidence in Neandertals and moderns. He concludes that while some differences are demonstrable, Neandertals appear to achieve craniofacial maturation at stages of dental maturation comparable to those characterizing modern humans. Williams asserts this result suggests fundamental patterns of human life history arose in an ancestor of archaic and modern *Homo*. Another factor that has engendered considerable interest concerns differences in Neandertal and modern energy requirements. Andrew Froehle, Todd Yokley, and Steven Churchill determine that the pattern of reduction in body size and in naso-facial morphology that distinguishes modern humans from archaic populations is almost certainly associated with a reduction in adult maintenance energy requirements, with potentially major consequences for reproductive success. Such differences, from their perspective, would have provided early modern humans who migrated into Europe with a distinct advantage in over the existing, larger-bodied Neandertals.

Without doubt, the most influential biological parameter largely absent from the 1984 volume is genetics. In the current volume, John Relethford considers the pattern of genetic variation and cranial variation in modern humans with an eye to understanding our origins. He concludes that both datasets support a primarily African origin of modern people but with small (but not insignificant) contributions from archaic peoples outside of Africa. John Hawks and Zach Throckmorton focus on the interpretation of the Neandertal and Denisovan genomes and the evidence of their contribution to modern Eurasians. They demonstrate that a single, large-scale bottleneck, as would result from a classic speciation event, is not compatible with existing genetic data and that a longer, more complex process of population interactions must have taken place between and among archaic and modern people. In addition to their contributions, essentially all of the regional papers have also discussed the impact of current genetic knowledge from both ancient and living populations to the perspectives now held on modern human origins.

Finally, papers by Rachel Caspari and Milford Wolpoff and by Erik Trinkaus provide a comparative assessment of biocultural changes occurring during the Late Pleistocene. Trinkaus finds that the only shifts associated primarily with early modern humans are reductions in the use of the anatomy for manipulation and in apparent stress levels. Most of the other changes seem to be related, directly or indirectly, to modern human population expansion with the early and then mid Upper Paleolithic, and existing information argues for only subtle differences in adaptive effectiveness among populations. Caspari and Wolpoff describe modernity as reflected in accelerated change and see this as an evolutionary pattern that differs from archaic patterns in both tempo and mode. They assert that the modern pattern, which begins with an increase in longevity and other evolutionary changes, is one of increasingly rapid genetic, biological, and social changes within a widespread, interconnected human species.

While we feel that all of the papers in this volume provide important viewpoints and consideration of the record of later human evolution, we certainly harbor no misconception that all pertinent biological perspectives are covered. We would like to have included more chapters written by more of our colleagues, but space limitations and our desire to have comprehensive regional papers precluded the possibility of including more than we have. We also recognize that some discussion of cultural factors, especially the changing ideas concerning the initial Upper Paleolithic (Châtelperronian and Uluzzian especially) and new discoveries relating to aesthetic expression in both Europe and Africa, would have been

valuable. Several authors do comment on these issues, but extensive coverage of the archaeological evidence would have certainly made the volume unwieldy.

Genetics and Genomics

There is no doubt that the most influential non-paleontological perspectives of later human evolution have been provided by the study of ancient DNA. From the first announcement of the isolation of a segment on Neandertal mtDNA in 1997, the potential of ancient DNA to shed light on modern human origins has been widely accepted. Beginning with this initial article (Krings et al., 1997), the consistent interpretation has been that Neandertal mtDNA haplotypes are not represented in modern humans (Caramelli et al., 2006, 2011). Still, Serre and colleagues (2004) pointed out that available mtDNA data could not rule out a small amount of Neandertal contribution to modern human gene pools. Similar suggestions were made by others based on various lines of genetic evidence (e.g., Relethford, 2001; Templeton, 2005; Eswaren et al., 2005).

In 2006, initial sequencing of Neandertal nuclear DNA was reported. While one study found no indication of a Neandertal contribution to early modern humans based on a sequence of 62,500 base pairs (Noonan et al., 2006), the other found something different. This second study, based on about a million base pairs, suggested that modern humans and Neandertals shared too many derived single-nucleotide polymorphisms (SNPs) to explain them as totally separate lineages that split several hundred thousand years earlier and remained completely separate (Green et al., 2006). Green and colleagues posited that low levels of gene exchange between Neandertals and modern humans following the split between these groups were probably responsible for their results. However, these results were widely criticized as the product either of statistical problems or contamination (Wall and Kim, 2007). Other Neandertal nuclear DNA studies soon provided interesting results, including demonstrations that Neandertals and modern people shared the same form of the important FOXP2 “language gene” (Krause et al., 2007) and that some Neandertals would have likely had lighter hair and skin pigmentation (Lalueza-Fox et al., 2007). It is also possible that modern humans might have gotten genetic material critical for development of a “modern” human level of neurological complexity from Neandertals (Evans et al., 2006). Although these examples are generally not explained as indicating any Neandertal contribution to modern human gene pools (Culotta, 2007; Lari et al., 2010), they might demonstrate just that (Cartmill and Smith, 2009). It is not surprising that Neandertal haplotypes may differ slightly from modern haplotypic variation, particularly given that modern human genetic patterns have changed appreciably since the Pleistocene. In fact we should not expect Neandertal and modern haplotypes to always be totally identical as long as the differences are not functionally relevant. Even given the slightly different haplotypes in Neandertals than those found in modern humans, the fact is that the earliest evidence of a character discovered in the fossil record is generally accepted, at least provisionally, as the origin of that character. That should be valid also for genetic features. If that premise is accepted, then the origin of these two important modern human traits may well lie in the Neandertal gene pool, as some aspects of the modern human immune system apparently do (Abi-Rached et al., 2011).

The most influential ancient human genetic work to date has certainly been the publication of the draft Neandertal genome (Green et al., 2010). This impressive accomplishment was based on segments derived largely from three small long bone fragments from Vindija and, not surprisingly, showed that Neandertals and modern humans were 99.8% identical genetically. More shocking for many scholars was that this study fundamentally confirmed the 2006 study by Green and his colleagues regarding the relationship between Neandertals

and modern humans, but with a bit of a twist. Green and colleagues' data show that Neandertals are more similar to modern Eurasians than to modern Africans and that Neandertals apparently contributed between 1% and 4% of the genetic material of modern Eurasians. This means Neandertals were not reproductively isolated from modern people in Eurasia, although they certainly were not the major source of the latter's gene pool. Still if a 1% to 4% Neandertal contribution survives in living human populations, it may well be that the original contribution to early modern populations was significantly larger. This is because we know there has been extensive change in modern human gene pools during and after the Pleistocene (see Cochran and Harpending, 2009), so much of the original Neandertal (and perhaps other archaic) contributions have been lost. While we believe the Neandertal and Denisova (Reich et al., 2010) genomic data are most commensurate with the assimilation model, a case perhaps could be made for a more classical version of multiregional evolution if the original contribution was indeed significantly larger.

A rather different explanation has been offered for this greater similarity of Neandertals to Eurasian moderns. Eriksson and Manica (2012) used simulation to demonstrate that the patterns documented by Green and colleagues might not be due to admixture between Neandertals and expanded moderns but might actually reflect common ancestry of these two lineages in Africa prior to the supposed speciation that resulted in the emergence of Neandertals in Eurasia. They argue that African populations prior to this split were "structured," meaning that they only exchanged genes with neighboring populations and thus maintained a considerable amount of genetic and morphological distinctiveness, at least in differing regions of Africa. Eriksson and Manica then assume that contact between Northern African and Eurasian populations was broken between 350 and 300 thousand years ago, leading to the evolution of Neandertals in Eurasia. However, the Northern African populations were likely to share SNPs with the populations that eventually evolved into Neandertals in Eurasia and also were more likely to represent the populations that moved into Eurasia as early modern people. Eriksson and Manica's simulations show that statistically this scenario is just as likely to result in the degree of shared SNPs that Green and colleagues interpret as being the result of hybridization between Neandertals and early modern populations.

It is important to remember that this is a statistically based scenario. It does not demonstrate that the original interpretation of introgression between Neandertal and early modern Eurasians is incorrect. It simply offers another possible explanation. In fact, analysis of linkage disequilibrium data in recent Europeans supports the recent interbreeding hypothesis rather than the genetic structuring model of Eriksson and Manica (Sankararaman et al., 2012). This study also indicates that introgression could have occurred anytime between 37 ka and 86 ka but most likely between 47 ka and 65 ka. The more recent dates might suggest that introgression could have occurred as early peoples first entered Europe, rather than in the Near East as previously thought (Green et al., 2010). If the new dating of the Kent's Cavern maxilla and the Grotta del Cavallo teeth establish modern humans in Europe by 41–45 ka that possibility is enhanced.

The Eriksson and Manica model does raise an important point. The two African genomes used by Green and colleagues were a San from Southern Africa and a Yoruba from West Africa. No African from North or East Africa was compared in this study. Even before the Eriksson and Manica study, it was clear that other African genomes were needed to be compared in order to substantiate the Green et al. conclusions (Smith, 2011). This situation is similar in principle to the genetic interpretation of mitochondrial DNA haplotypes in Neandertals, early modern Europeans, and more recent populations. Neandertal mtDNA haplotypes do not fall in the range of modern human haplotypes, and early modern Europeans do fall in that range. This was widely hailed as proof that Neandertals were a different species than modern humans and did not contribute to their ancestry (Klein, 2009).

However, although there was no evidence for a Neandertal contribution, the limited number of early modern specimens ($N = 7$) made it statistically impossible to rule out a Neandertal contribution of up to 25% (Serre et al., 2004), far higher than the Neandertal genome data suggests. In fact to rule out a Neandertal contribution of $\leq 5\%$, a sample of sequences greater than the number of all known early modern European skeletons would be needed! Critiques of earlier genetic studies arguing for total replacement of Neandertals by the senior editor (Smith et al., 2005; Weiss and Smith, 2007; Cartmill and Smith, 2009) focused on the limitations of relatively small sample size in the ancient mtDNA studies and stressed the interpretation of Serre and colleagues (2004) that small sample sizes did not allow exclusion of a relatively small Neandertal contribution to modern humans. Given this, it would be an inexcusable inconsistency to claim that the issue of Neandertal contribution to modern Eurasians has been solved by the 2010 analysis of the Neandertal genome. In fact, even if the SNPs that reflect Neandertal-modern Eurasian similarities are not found when several North or East African genomic samples, it will still not disprove conclusively the Eriksson-Manica scenario. There will still linger the specter of small sample size.

Finally, there are now arguments that genetically modern humans left Africa after anatomically modern humans, so that the earliest evidence of modern human skeletons does not represent the earliest evidence of genetic modernity. For example, Macaulay and colleagues (2005) assert that genetically modern people left Africa around 60,000 years ago and very quickly spread throughout the coastal regions of Asia, all the way to Southeast Asia. Only after this do they spread north into the Near East and ultimately into Europe. This must be, of course, several tens of thousands of years after the first Skhül-Qafzeh people were in the Near East. Other studies see this process as a bit more complicated but still occurring after the first anatomically modern people have left Africa (see Gibbons, 2011). Some morphological studies have also identified morphological evidence of this latest “out-of-Africa” migration phenomenon (Grine et al., 2007; Crevecoeur et al., 2009). While we do not find the morphological evidence compelling, we certainly believe that the modern human gene pool in Eurasia has been altered substantially since the first morphologically modern people arrived. Despite the indication that these changes were substantial (Cochran and Harpending, 2009), we have yet to see a claim that such late genetic changes must reflect another speciation event in later human evolution.

From our perspective, the ancient DNA from Vindija and Denisova is best interpreted within the framework of assimilation, as are the morphological data. There is great excitement over the ancient DNA from these samples, and rightly so. The sequencing of these genomes is an incredible scientific accomplishment and provides data of inestimable value. However, the genetic data also have limitations and are open to differing interpretations. This often stems, especially in the study of ancient DNA, from a problem that also haunts paleontology—sample size. Thus it is unlikely that genetics alone will resolve current controversies concerning modern human origins, no matter how much more reliable genetic studies are perceived to be. The importance of morphology cannot be subsumed by the excitement of genetic breakthroughs. Rather the genetic and morphological evidence must both continue to play equally important roles in our search to explain the biological beginnings of people like us.

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Chapter 1

Africa: The Cradle of Modern People

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This chapter is intended as a survey of the African fossil record relevant to the origin of modern humans. This record has been summarized in detail fairly often over the four decades (e.g., Howell, 1978, 1994; Klein, 1989, 1999, 2009; Cartmill and Smith, 2009; Smith et al., 1989; Wolpoff, 1996; Bräuer, 1984a, 1984b, 1989, 1991, 1992, 2001a, 2001b, 2007, 2008; Bräuer and Rimbach, 1990; Stringer, 2002, 2011; Rightmire, 1976, 1978a, 1978b, 1984a, 1991, 1992, 1994, 1998, 2001a, 2008, 2009), so the present chapter will seek to cover some of the more recent and smaller finds in more detail while providing a basic overview of the better-known finds. Also considered are some of the attendant issues that surround human evolution during the Middle to Late Pleistocene. These issues include speciation, the impact of genetic data, and the role of climate in the human evolution in Africa.

Within 5 years of the publication of Smith and Spencer's *The Origins of Modern Humans: A World Survey of the Fossil Evidence* in 1984, knowledge of the timing and pattern of key events in the origin and spread of modern humans had increased substantially. The most plausible interpretation of new data from mitochondrial DNA (mtDNA) was that a common ancestor (a mother in this case) of all modern human mtDNA sequences had lived in Africa between 200,000 and 100,000 years ago (Cann et al., 1987; Stoneking and Cann, 1989; Delson, 1988). These initial findings were confirmed and refined by subsequent studies (Vigilant et al., 1991; Stoneking et al., 1992). At the time, these findings were subjected to criticism by multiregionalists (e.g., Wolpoff, 1989; Smith et al., 1989; Frayer et al., 1993) and some geneticists (Templeton, 1991, 1993, 1996, 1997). Nevertheless, the findings from mtDNA were supported by some early, worldwide analyses of polymorphisms in human proteins and blood groups (Jones and Rouhani, 1986; Wainscoat et al., 1986, 1989; Nei and Roychoudhury, 1982, 1993), which also showed a likely African origin of modern humans and a divergence time on the order of 100,000 years between populations, although other contemporary analyses suggested a different pattern (e.g., Excoffier et al., 1987).

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It proved to be more difficult to find and characterize patterns of DNA sequence variation in human Y chromosomes because the vast majority of the sequence was identical between individuals, but once researchers began to identify polymorphic sites, Y chromosomes showed a very similar pattern to mtDNA (Lucotte, 1992; Hammer, 1995; Hammer and Horai, 1995; Pääbo, 1995; Jobling and Tyler-Smith, 1995; Hammer and Zegura, 1997; Hammer et al., 1997; Seielstad et al., 1999). Early estimates were that the variation present in human Y chromosomes inferred the coalescent age for the most recent common ancestor to be around 50–100 ka, most likely in Africa (Hammer, 1995). The most recent analysis of a larger dataset indicates the common ancestor lived 141.5 ± 15.6 ka in Africa (Cruciani et al., 2011). An African origin of Y chromosomes has continued to be supported in later analyses (Underhill et al., 2001; Semino et al., 2000, 2002; Kayser et al., 2001, 2004; Ke et al., 2001; Tyler-Smith, 2002; Tishkoff et al., 2007; Karafet et al., 2008). Additional analyses of Y chromosomes have demonstrated that after a Late Pleistocene dispersal from Africa, some men returned to the continent from Eurasia (Hammer et al., 1998; Cruciani et al., 2002). This back migration may be linked with the spread of modern humans across Northern Africa (Olivieri et al., 2006).

At the same time that genetic studies were amassing new insights, advances in dating using electron spin resonance (ESR), uranium-series (U-series) dating, thermoluminescence (TL), optically stimulated luminescence (OSL), amino acid racemization on ostrich eggshell (Miller et al., 1999), and, to a lesser extent, obsidian hydration (e.g., Clark et al., 1984) began to raise the curtain on events lying beyond the limit of radiocarbon and to provide an absolute chronology for Middle Paleolithic (MP) from Eurasia and Middle Stone Age (MSA) sites from Africa. Early and influential applications of these novel methods demonstrated that the Israeli sites of Skhül and Qafzeh, which both contained multiple interred skeletons of nearly modern humans (McCown and Keith, 1939; Howell, 1958; Vallois and Vandermeersch, 1972; Vandermeersch, 1981; Trinkaus, 1984), were older, dating to 80–120 ka (Valladas et al., 1988; Schwarcz et al., 1988; Mercier et al., 1993, 1995), than the Neandertals from the Levant, most of which dated to around 60 ka (Valladas et al., 1987; Schwarcz et al., 1989; Mercier et al., 1995; Grün and Stringer, 2000). These dates confirmed Bar-Yosef and Vandermeersch's (1981) deduction of the age of the hominins from Qafzeh and overturned arguments that Neandertals had evolved into modern humans in the Levant by 50 ka (e.g., Trinkaus, 1984).

By the late 1980s, new genetic data, new dates, and new discoveries of fossils had combined to reinforce the synthesis presented earlier that modern humans had evolved early in Africa and subsequently spread to the rest of the world (Rightmire, 1984a; Bräuer, 1984a, 1984b; Stringer and Andrews, 1988; Cavalli-Sforza et al., 1988). This conclusion was based on the age of Omo I (Day, 1969) and championed later by Rightmire (1979, 1981) and Beaumont, de Villiers, and Vogel (Beaumont et al., 1978; Beaumont, 1980; de Villiers, 1973, 1976) for the Border Cave fossils, and Singer and Wymer (1982) for the hominins from Klasies River Mouth.

In Africa, application of some of the new dating techniques made it clear that the archaeological contexts for the hominins from Border Cave and Klasies River Mouth (Klasies River) dated to 70–120 ka (Grün et al., 1990a, 1990b; Grün and Stringer, 1991; Grün and Beaumont, 2001; Grün et al., 2003, 2005), although controversy remained over the issue of whether all of these hominins were contemporaneous with the archaeological sediments that had been dated. Nevertheless, these absolute ages confirmed inferences from the geology and stratigraphy of the sites that the MSA in both had to be older than the limit of radiocarbon (Vogel and Beaumont, 1972; Butzer, 1978, 1984; Butzer et al., 1978; Beaumont et al., 1978) and corroborated earlier K-Ar and

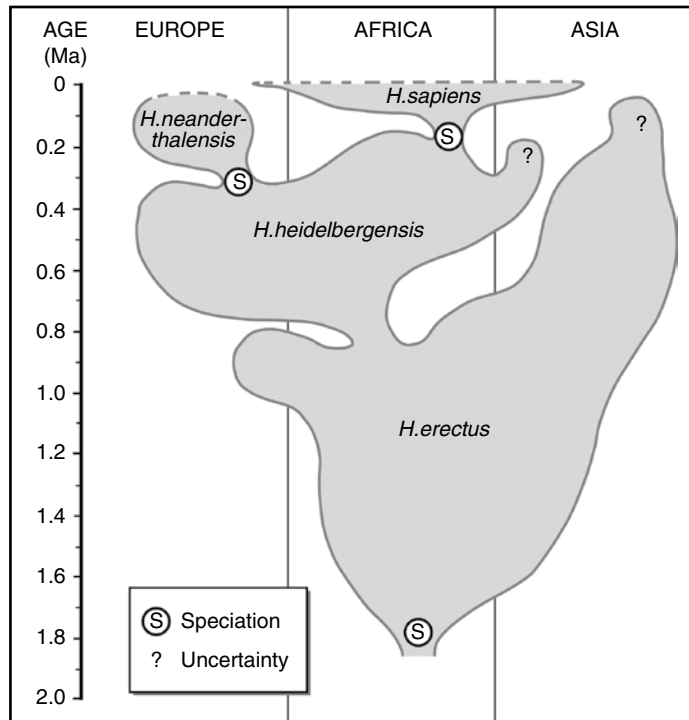


Figure 1.1. Rightmire's phylogeny (after Rightmire, 1998).

uranium-series dates of Middle Stone Age sites such as Evernden and Curtis's (1965) 240 ka K-Ar date for the MSA site Malawa Gorge, the geological, radiocarbon, and uranium-series dates for the Omo-Kibish sequence (Butzer, 1969; Butzer et al., 1969; Butzer and Thurber, 1969), and Wendorf et al.'s (1975) date of 180 ka for the MSA site of Gademotta in Ethiopia. The rapid accumulation of absolute dates confirmed the antiquity of the MSA and placed it on center stage as the cultural milieu for the origin of modern humans (Clark, 1988, 1989, 1992; Klein, 1989, 1999, 2009; McBrearty and Brooks, 2000).

Turning to the African fossil record itself, by the mid-1980s, researchers had established a broad outline of later hominin evolution in Africa that remains the consensus today (Rightmire, 1984a, 2008; Bräuer, 1984b, 2008) (Figures 1.1 and 1.2). Figure 1.1 shows Rightmire's (1998) phylogeny. Figure 1.2 shows a recent version of Bräuer's (2008) division of the Pleistocene African fossil record into a series of morphological grades leading to anatomically modern *Homo sapiens* between 200 and 150 ka.

This consensus model of later hominin evolution in Africa generally emphasizes a continuous, anagenetic process of evolution and builds upon earlier syntheses (e.g., Howell, 1978). The model starts with the establishment of *Homo erectus* throughout the habitable portions of the continent (i.e., areas not covered by deserts or the tropical forests of the Congo Basin) between 1.5 and 1.0 Ma. Due to the finds from Dmanisi and more precise, absolute dates for early hominin sites in Israel, southern China, and Indonesia, anthropologists now know that some populations of *Homo erectus*

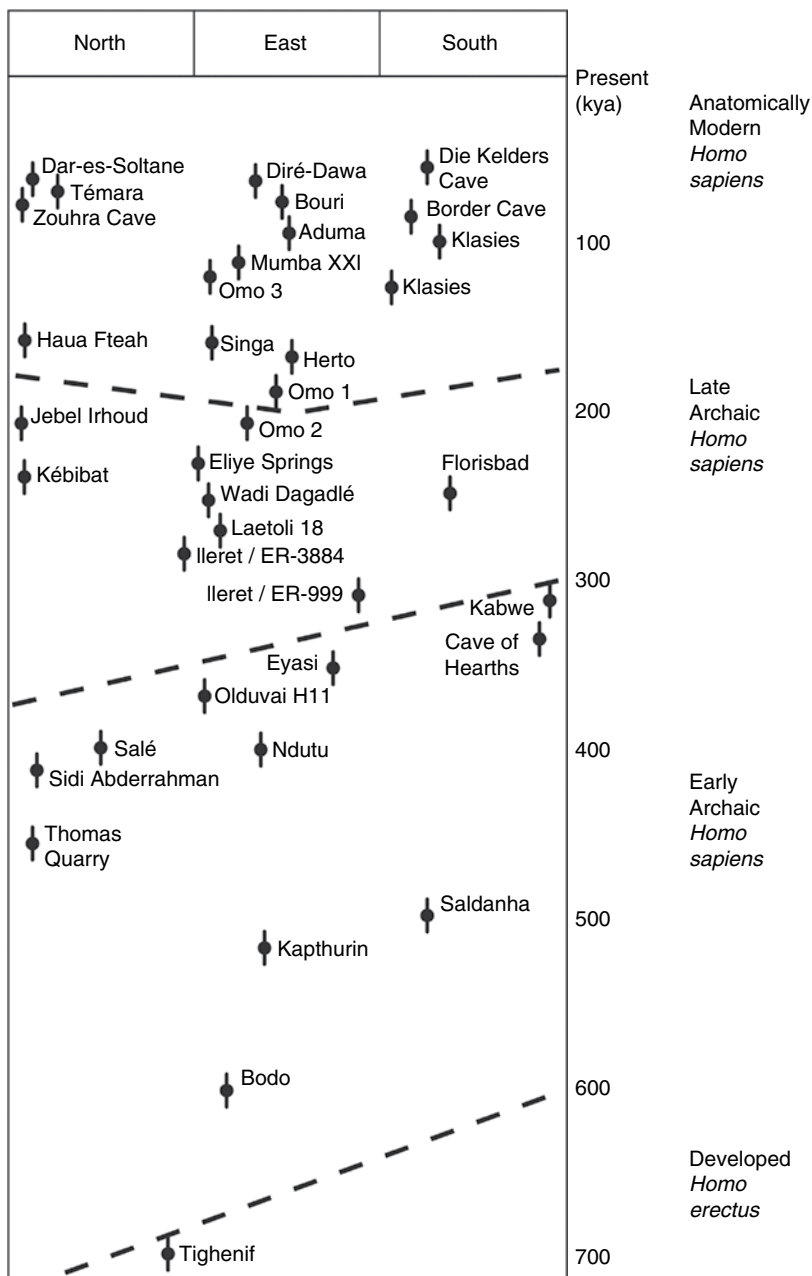


Figure 1.2. Bräuer's grades of *Homo sapiens*, from Bräuer (2008), courtesy of Günter Bräuer.

(or, perhaps, an even more primitive species such as *Homo habilis*) spread from Africa into Eurasia by 1.8–1.9 Ma, almost doubling the widely held view for the duration of human occupation outside of Africa that had seemed likely in the mid-1980s (Klein, 1989). The populations of *Homo erectus* that reached China and the island of Java changed only subtly in cranial morphology over the next million to million and a half years, allowing

many experts to group the Asian specimens together with early African fossils as members of a single species (Santa Luca, 1980; Rightmire, 1981, 1990, 1991; Walker, 1993; Gilbert et al., 2003; Gilbert, 2008a). By 1.0 Ma in Africa, the hominin cranium from the Danakil Depression in Eritrea shows evidence of evolution toward a more modern architecture with more vertical parietals (Abbate et al., 1998). The nearly contemporary cranium from the Daka Member of the Middle Awash fits more broadly within the hypodigm of *H. erectus* and possesses a mosaic of features that had formerly been argued to be more typical of Asian or African members of the species (Asfaw et al., 2002; Gilbert et al., 2003). As such, it cautions against placing too much emphasis on the importance of those regional differences, and tends to reinforce notions of the fundamental morphological homogeneity of the species (Asfaw et al., 2008; Gilbert et al., 2003, 2008; Gilbert, 2008a).

The next widely recognized stage in the emergence of modern humans involves the appearance of a larger-brained hominin between 800 and 600 ka that different authors call early archaic *Homo sapiens*, *Homo heidelbergensis*, *Homo rhodesiensis*, or perhaps *Homo antecessor* (Figure 1.2). By 230–300 ka a new form had evolved with a vertically shorter face, smaller browridges, and diminished angulation of the upper and lower tables of the occipital. This form is often called late archaic *Homo sapiens* or *Homo helmei*, although as Bräuer (2008) explains in detail, authors disagree about which specimens belong in the group and which do not. The last phase involves the first appearance of anatomically modern *Homo sapiens*, which makes its first appearance between 200 and 150 ka in the Ethiopian sites of Omo-Kibish and Herto (McDougall et al., 2005, 2008; Brown and Fuller, 2008; White et al., 2003; Clark et al., 2003). These dates are substantially earlier than the earliest date envisioned in the late 1980s, when the 130 ka uranium-series date for Omo I and II was repeatedly contested by multiregionalists (Wolpoff, 1989; Frayer et al., 1993) and proponents of the assimilation model (Smith et al., 1989; Smith, 1993), as documented in detail by Fleagle et al. (2008). Wolpoff (1989: 65) essentially dismissed the dates, writing:

The Omo radiometric dates have been continuously disputed ever since their first publication because radiocarbon determinations based on shells are notoriously inaccurate, and recent Uranium/Thorium dates are problematic. Various faunal and stratigraphic “dates” have been suggested as replacements for these radiometric estimates (Day, 1972; Stringer, 1989) and according to these the age of the three fossils could range between 40,000 and 130,000 years. However, which of the various date estimates may be correct cannot be established, and the fact is that there is no particular reason to accept any of them as valid!

In contrast, contemporary proponents of various versions of a Recent African Origin Model for the origin of modern humans generally accepted that Omo-Kibish I and II had to be approximately 100,000 years old, and possibly older.

Rather than repeat the basic descriptions of the large number of fossil specimens that make up the fossil record for the emergence of modern humans in Africa (Figure 1.3), this review concentrates on new fossil finds and other developments that have occurred since the summaries of the African evidence by Rightmire (1984a), Bräuer (1984b), and Hublin (1985, 1992). Howell (1994, 1999), Bräuer (2008), and Rightmire (2008) have written recent updates to their earlier syntheses, and recent paleoanthropological textbooks, especially Klein (2009) and Cartmill and Smith (2009), present overviews of the material, and most of the fossil specimens are also described and pictured in Schwartz and Tattersall (2003).



Figure 1.3. Map of Africa showing the key hominin sites from Bräuer (2008), courtesy of Günter Bräuer.

Homo erectus

Little controversy surrounds the idea that early African *Homo erectus* (or *Homo ergaster*, if the early African examples of the taxon constitute a separate species) forms the starting point for the evolutionary lineage that ultimately led to *Homo sapiens*. Rightmire's (1990) synthesis of the available fossil evidence and the publication of the monograph on the Nariokotome skeleton, as well as the discovery of the Dmanisi hominins (Vekua et al., 2002; Antón, 2003; Lordkipanidze et al., 2005, 2006, 2007; Rightmire et al., 2006b, 2008; Skinner et al., 2006; de Lumley et al., 2006; Wallace et al., 2008; Pontzer et al., 2009), stand as important milestones in our understanding of this species. A number of other important discoveries of fossils of African *H. erectus* were made in the 1990s and 2000s, including a left half of a mandible, parietal, frontal, occipital, and four isolated teeth from Konso in southern Ethiopia (Suwa et al., 2007), all of which are associated with an early occurrence of the Acheulean dated to 1.6 Ma (Asfaw et al., 1992). Exploration of the Daka Member at Bourri in the Middle Awash led to the discovery of a calvaria, cranial fragments from two other individuals, a left tibia lacking its distal end, three partial femora, a talus, and a partial mandible (Asfaw et al., 1992, 2008; Gilbert et al., 2008; Gilbert, 2008b). Research at Lainyamok in the Kenyan Rift Valley produced four hominin fossils, a left femoral diaphysis and three teeth

(right P⁴-M²). All were collected from Middle Pleistocene sediments that date to 0.70–0.53 Ma on the basis of a K-Ar date for an overlying tuff and the presence of a more modern fauna than that of Members 1–7 at Olorgesailie (Shipman et al., 1983; Potts et al., 1988). The femoral fragments from Daka and Olorgesailie resemble fossils attributed to *H. erectus* from East Turkana (Day and Leakey, 1973; Day, 1976) and Bed IV at Olduvai Gorge (Day, 1971). The femora of *Homo erectus* generally have thick cortical bone and a greater medio-lateral than antero-posterior diameter at midshaft that distinguish *H. erectus* femora from the great majority of living humans (Kennedy, 1983, 1984, 1985, 1992).

KNM-ER 42700

Other and recent developments in the study of *Homo erectus* in Africa include the discovery in East Turkana of KNM-ER 42700 (Spoor et al., 2007), a fully adult but remarkably small calvaria with a cranial capacity of only 691 cc. The specimen dates to 1.55 Ma. Another specimen (KNM-ER 42703) announced in the same publication is a right maxilla attributed to *H. habilis*, which dates to 1.44 Ma and suggests the two taxa of early *Homo* overlapped in the Turkana Basin for ~0.5 Ma (Spoor et al., 2007). KNM-ER 42700 may simply be an extreme manifestation of the allometric pattern described by Antón et al. (2007) in which larger crania of *H. erectus* tend to have larger browridges, more sagittal keeling, and development of other cranial superstructures. However, based on the patterns present in a geometric morphometric analysis of available *H. erectus* crania (Baab, 2008a), KNM-ER 42700 may belong to a different taxon (Baab, 2008b).

KNM-OL 45500

Research in an upland sector of Olorgesailie led to the discovery of a second very small *H. erectus* cranium, KNM-OL 45500 (Potts et al., 2004), which dates to 0.97–0.90 Ma. Only the frontal part of the cranium is preserved, but enough survives so that Potts et al. (2004) could estimate the cranial capacity at around 650–780 cc. Although small, this endocranial capacity is similar to OH 12 and Dmanisi D2282 and D2280. Its late date coupled with its small size, however, suggest that populations of *H. erectus* either featured a striking amount of individual variation or were more sexually dimorphic than Walker (1993) had concluded in his assessment of the Nariokotome skeleton and other available data.

Gona Pelvis

Simpson et al. (2008) described a female *H. erectus* pelvis from the Busidima Formation in Gona, Ethiopia. The pelvis dates between 1.7 and 0.7 Ma. Contrary to expectations (Ruff and Walker, 1993), the Gona pelvis is very broad like later Middle Pleistocene pelves from Atapuerca (Arsuaga et al., 1999; Bonmatí et al., 2010) but has a small acetabulum, implying a short stature of 120–146 cm (Simpson et al., 2008). Also contrary to expectations, it features large dimensions of its birth canal. Ruff (2010) argued that the body mass (~33 kg) predicted from the acetabulum is substantially lower than that derived from any other femoral head or acetabulum attributed to *H. erectus* and thus the Gona pelvis might derive from an australopith. Simpson (personal communication) rejects this interpretation; the only craniodental fossils known from the Busidima Formation are of *H. erectus*.

In the 1990s, the brain size in *H. erectus* suggested a life history almost precisely midway between chimpanzees and australopiths and modern humans (B. H. Smith, 1993, 1994).

Examination of enamel microstructure of the teeth of *H. erectus* specimens showed a faster pattern growth and development in *H. erectus* than expected based on brain size (Dean et al., 2001; Dean and Smith, 2009), with maturation in *H. erectus* closer to one-third of the way from a chimpanzee-like pace to a human-like one rather than halfway. A similar acceleration in the tempo of maturation appears to be evident in postcranial growth (Graves et al., 2010). Some of the new studies and finds of *H. erectus*, especially the Gona pelvis and the revised estimates of the rate of maturation of KNM-WT 15000, suggest that *H. erectus* may not have been either as static over evolutionary time or as human-like as the available evidence led Walker (1993) to conclude.

The Transition to *Homo heidelbergensis* or “Archaic *Homo sapiens*”

By 600 ka, the Bodo cranium shows a clear change in morphology in the form of a larger cranial capacity of around 1,250 cc (Conroy et al., 2000). A series of other, morphologically similar hominins such as Kabwe (Broken Hill) and Saldanha share a similarly large brain. Coincident with the larger cranial capacity are higher and more vertical parietal bones, a higher temporal squama, and a coronally broader frontal bone (Conroy et al., 1978, 2000; Adefris, 1992; Rightmire, 1996, 2008; Bräuer, 2008). Unfortunately, very few fossil hominins are known from sub-Saharan Africa for the period between the Buia and Daka crania at 1.0 Ma and Bodo at 0.6 Ma.

The gap in the African hominin fossil record for between 1.0 and 0.6 Ma is further complicated in that more complete fossil evidence is now known from Europe in the form of *Homo antecessor* (Bermúdez de Castro et al., 1997, 1999, 2003; Carretero et al., 1999; Lorenzo et al., 1999; Rosas and Bermúdez de Castro, 1999; Manzi, 2004; Martínón-Torres et al., 2007; García-González et al., 2009; Gómez-Olivencia et al., 2010). The existence of *H. antecessor* poses new questions about the pace and mode of evolution away from the morphology of *H. erectus*. If *H. antecessor* is a viable ancestor of later European and African hominins, an important step in hominin evolution must have occurred between 1.0 and 0.8 Ma, but much remains to be learned about this evolutionary transition (Rightmire, 1998; Stringer, 2003).

The primary criticism that has been leveled at *H. heidelbergensis* as a distinct, new species is that no unified set of features exists that can be used to diagnose it throughout its existence. Many specimens placed in the taxon by some researchers lack or have equivocal traces of one or more of the features that characterize Bodo, Kabwe, and Petralona (Wolpoff, 1993, 1996). However, a recent geometric morphometric study of available crania by Harvati et al. (2010) demonstrates that, in fact, early Middle Pleistocene European and African hominins share substantial similarities in the morphology of their face, temporal bone, and posterior cranial vault. The morphology of these areas diverged after MIS 7 (Marine Isotope Stage 7), supporting the view (Hublin and Tillier, 1992) of a gradual accretion of Neandertal features in Europe and modern traits in Africa.

Two other specimens that likely belong among early archaic African hominins, the partial mandible from Kanam, Kenya (Tobias, 1960), and the partial cranium from Salé in North Africa (Hublin, 1985, 1992), display pathologies that hinder an unambiguous assessment of their affinities to other specimens in the group and are not considered in more detail here.

Bodo

The partial cranium from Bodo was discovered in 1976 (Conroy et al., 1978; Kalb et al., 1980). Later work at the site by the Middle Awash project clarified some details of the stratigraphy and collected a thick-walled parietal of a second hominin (BOD VP 1/1) (Asfaw,

1983) and a fragment of a distal humerus (BOD VP 1/2) (Carretero et al., 2009). Importantly, the Middle Awash project was also able to obtain a K-Ar date of 600 ka for these hominin remains (Clark et al., 1994).

The Bodo cranium is massive, with a vertically thick and highly projecting browridge, large orbits, a wide interorbital distance and pyriform aperture, and a very broad and tall midface. Conroy et al. (1978) presented a detailed initial description of the cranium, and Adefris (1992) wrote the first comprehensive description of it. Rightmire (1996) followed with an evaluative description, arguing that the cranium differed from *H. erectus* and likely provided evidence that speciation had taken place within *Homo* during the Middle Pleistocene of Africa. Kappelman (1996) predicted a body mass for Bodo of approximately 117 kg from its orbital area.

In the process of cleaning the cranium, White (1985, 1986) noted the presence of a series of fine cutmarks on the frontal and around the orbit, apparently made by stone tools around the time of death rather than a metal implement after discovery of the fossilized remains. Conroy et al. (2000) used volumetric reconstruction of the cranium from CT scans to estimate the cranial capacity as of around 1250 cc, with a probable range of 1200–1325 cc, depending upon how the base and posterior of the cranium are reconstructed. Copies of CT scans of the specimen are available to researchers through the Digital Archive of Fossil Hominoids of the Department of Anthropology at the University of Vienna (Seidler et al., 1999).

A partial left parietal (BOD-VP-1/1) from a second individual was collected by T. White in 1981 320 m SSW of the cranium's find-spot during a visit to the site (Asfaw, 1983). The fragment has thick diploë, a pronounced angular torus, and a prominent extension of the supramastoid crest (Asfaw, 1983). These features are commonly encountered in *H. erectus* and, among Middle Pleistocene hominins, could be considered primitive.

The humerus from Bodo (BOD VP 1/2) consists of a distal left shaft that lacks its articular surface (Carretero et al., 2009). Like the distal humeri from other Middle Pleistocene hominins, it has a wide olecranon fossa and comparatively narrow medial and lateral pillars flanking the fossa (Carretero et al., 2009). Carretero and colleagues used regressions based on recent human samples and the Sima de los Huesos sample to estimate the bi-epicondylar breadth of BOD VP 1/2, obtaining a probable value of 62–63 mm, which falls near the middle of the Sima de los Huesos sample, suggesting it belonged to an average-sized individual rather than a small one as originally reported (Clark et al., 1994).

Saldanha

Other possible examples of *H. heidelbergensis* include the calotte from Saldanha (also known as Elandsfontein or Hopefield) (Drennan, 1953; Drennan and Singer, 1955; Singer, 1954; Singer and Wymer, 1968). Saldanha has long been likened to Kabwe, which it resembles closely. While there has been a considerable amount of archaeological work on Acheulean sites around Saldanha Bay since the 1980s (e.g., Klein et al., 2007), there have been few new investigations focused on the hominin calotte or mandibular fragment.

Kabwe

The well-known and exquisitely preserved fossils from Kabwe (Broken Hill) in Zambia comprise a cranium, maxilla of a second individual, two proximal femora, two femoral diaphyseal fragments, a distal femur bearing its condyles, a humerus, complete tibia, sacrum, and fragmentary innominate. The cranium was described as the type specimen of *Homo rhodesiensis* (Pycraft et al., 1928), and probably a geographic or individual variant of the same hominin species or lineage represented by Bodo (Rightmire, 1984a, 1996, 1998, 2008; Bräuer, 1984b, 2008), whether one calls that lineage *H. heidelbergensis*, *H. rhodesiensis*, or something else.

Obtaining a precise age for the Kabwe cranium and other remains has proven difficult, with dates based on fauna and archaeological associations placing the specimen around 120–300 ka (e.g., Klein, 1999). Recent ESR dates on a chip of enamel from one of Kabwe's teeth indicate a date between 300 and 200 ka, with more likelihood of an age closer to the younger limit of the range (Stringer, 2011). Thus despite the archaic morphology of the cranium, it now appears to have been penecontemporaneous with morphologically more advanced specimens like Florisbad and KNM-ER 3884.

Since the 1980s, there have been a number of new morphological analyses of these fossils. Stringer (1986) noted that the innominate fragment had greatly thickened cortical bone on the acetabulo-cristal buttress, an archaic trait that makes it resemble OH 28. Calcagno and Gibson (1992) revisited the remarkable tooth decay evident in the cranium, as did Bartsiokas and Day (1993), who speculated that lead poisoning could have contributed to the decay. In comparisons to the Berg Aukas femur, both proximal femora from Kabwe are much more similar to modern humans (Grine et al., 1995; Pearson, 1997), which agrees with Kennedy's (1984) observations that the Kabwe femora had fundamentally modern morphology. Kappelman (1996) predicted a body mass for the Kabwe cranium of approximately 118 kg based on its orbital area. CT scans of Kabwe highlighted the vast extent of its paranasal sinuses and facilitated comparisons of other endocranial details (Seidler et al., 1997).

Yokley and Churchill (2006) included the E.898 humerus from Kabwe in a morphometric analysis of distal humeri, concluding Neandertals could be distinguished from recent humans but the Kabwe specimen could not. Trinkaus (2010) presented an analysis of the Kabwe tibia, concluding it came from a tall individual but one of uncertain body mass, with a range of 63.7–81.1 kg, depending on the ecogeographic adaptations that one assumed. It also has a retroverted tibial plateau and a blunt anterior crest, traits it shares with other archaic tibiae.

Ndutu

The small cranium from near Lake Ndutu in Tanzania (Mturi, 1976; Clarke, 1976, 1990; Rightmire, 1983) has generally been included in the same group or grade as Bodo, Kabwe, and Saldanha. Ndutu is imprecisely dated by tuff correlation with the upper part of the Masek Bed at Olduvai (Rightmire, 1983); most authorities favor an age of around 400 ka, give or take 100 ka. The cranium is small in overall size and fragmentary; Holloway and Rightmire estimated its brain size to be between 1,070 and 1,120 cc (Rightmire, 1983). The cranium is broadest across the supramastoid crests, but the parietals rise almost vertically above them (Rightmire, 1983). The upper and lower tables of the occipital are less angled than in *H. erectus* and more comparable to Kabwe and later specimens (Rightmire, 1983). The preserved portions of the supraorbital tori project strongly from the squama of the frontal but are vertically thin. Although fragmentary, the face must have been vertically short (Clarke, 1990).

Manega (1993) worked to clarify the age of the Ndutu Beds at Olduvai, obtaining four single crystal laser fluorescence $^{40}\text{Ar}/^{36}\text{Ar}$ dates for samples from tuffs in the upper Ndutu Beds spanning 0.21 ± 0.02 Ma to 0.45 ± 0.04 Ma, with a bulk weighted mean of 0.23 ± 0.01 Ma.

CT scans of Ndutu are available from the University of Vienna's database of fossil hominins.

Baringo Kapthurin

McBrearty and colleagues' excavations in the Kapthurin formation at Lake Baringo, Kenya, have provided some of the best-documented and most influential work on the late Acheulean

and earliest MSA cultural context for Middle Pleistocene *Homo* in Africa. Work in the 1960s by Margaret Leakey (Leakey et al., 1969) led to the discovery of a mandible (KNM-BK 8518) attributed to *H. erectus* (although in Africa, there seem to be few, if any, differences in the mandibles of *H. erectus* and Middle Pleistocene *Homo*), a right ulna lacking its distal end, a slender right first metatarsal, and two proximal manual phalanges (Solan and Day, 1992; McBrearty et al., 1999). McBrearty's more recent research has provided more precise dates for the hominin fragments as well as the earliest known chimpanzee fossils, three teeth that date to between 284 ± 12 ka and 545 ± 3 ka (and likely much closer to the older age based on stratigraphic position) (McBrearty and Jablonski, 2005). Solan and Day (1992) described the right ulna (KNM-BK 66) from the Kapthurin Formation, from levels dating to 510–512 ka (Deino and McBrearty, 2002). The specimen is long, slender, has only weakly imprinted muscle origins and insertions, and has a relatively low coronoid process, a primitive feature in later *Homo* that also occurs in Neandertals and some specimens of early “modern” humans from the MSA (Churchill et al., 1996; Pearson and Grine, 1996). The archaeological record from the Kapthurin Formation has produced a series of surprises, including sites with evidence of precociously early production of blades as early as 500 ka (Johnson and McBrearty, 2010) and evidence of a technological transition to the MSA as early as 285 ka (Tryon and McBrearty, 2002).

Berg Aukas

New hominin fossils discovered or described since the mid-1980s that may belong to *Homo heidelbergensis* (or other Middle Pleistocene *Homo*) include a proximal femur from Berg Aukas in Namibia and a tibia and teeth from Hoedjiespunt in the Western Cape of South Africa. Berg Aukas is a massive proximal half of a right femur that has a very large head that measures 56.4 mm vertically, a low neck-shaft angle, and very thick cortical bone (Grine et al., 1995). The femur was recovered from deep underground in a mine in 1965, and its stratigraphic associations were not studied in detail at the time (Grine et al., 1995). Its antiquity remains uncertain. Its morphology most closely recalls Neandertals from Europe. Its original length is estimated at 518 mm, which would correspond to a tall stature, and the large head predicts a mass of ~93 kg (Grine et al., 1995). A later analysis by Trinkaus et al. (1999) argued the femur came from a tropically adapted human based on subtrochanteric shape and diaphyseal robusticity.

Hoedjiespunt

Remains that may derive from Middle Pleistocene hominins came from a small assemblage of bones that were found eroding from an ancient hyena den in eolian sand dunes lining Saldanha Bay in the Western Cape Province, South Africa (Berger and Parkinson, 1995, 1997). Teeth from the site include two maxillary molars (a left M^2 and right M^3) and a left central and left lateral mandibular incisor (Berger and Parkinson, 1995; Stynder et al., 2001). All of the teeth belonged to a subadult and are larger than homologous teeth of living Africans but similar in size to those of African and European Middle Pleistocene hominins. The tibia from the site consists of most of a right shaft, preserved from just below the tibial tuberosity to the distal metaphysis. Like other archaic tibiae, it has a blunt and straight anterior crest (Churchill et al., 2000). Its original length was estimated at more than 360 mm; body mass predicted from the bone is in excess of 60 kg (Churchill et al., 2000). Micromammals from the site, which were likely consumed and deposited by barn owls, show a habitat similar to today but perhaps more arid (Matthews et al., 2005).

The excavators of Hoedjiespunt place it between 200 and 350 ka; it seems to have been associated with a period of low sea level, possibly MIS 8 (Churchill et al., 2000). However,

Butzer (2004) has argued that the hominin fragments and other fossils may actually derive from the neighboring Late Pleistocene site of Sea Harvest and were redeposited by the action of road grading in the 1970s and 1980s. An effort to directly date these hominins is needed.

Late Archaic/Transitional Specimens

Hominins similar to Bodo persisted in Africa until around 300ka, and possibly until 200ka (Stringer, 2011). The tempo and mode of transformation to Bräuer's next grade, late archaic *Homo sapiens*, which had occurred by between 300 and 230ka, remains unclear. The "late archaic" group is populated by an abundance of finds including Florisbad, Eliye Springs, KNM-ER 3884, KNM-ER 999, Ngaloba (Laetoli Hominid 18), Jebel Irhoud 1-4, Wadi Dagladlé, Kébibat (Rabat), and Omo II (Bräuer, 1984b, 2008; Rightmire, 1984a, 2008). They present a substantial amount of variation in browridge size and morphology, ranging from fairly large, protruding browridges (e.g., Florisbad, Ngaloba, and KNM-ER 3884) to more reduced forms (e.g., the preserved portions of Omo II and Jebel Irhoud 2). They also show a wide range of variability in occipital morphology from substantial reduction in angulation between the upper and lower tables and weak development of the occipital torus (e.g., Ngaloba) to a strongly angled form that is reminiscent of *Homo erectus* (e.g., Omo II). In some cases, these specimens show temporal overlap with the earliest modern humans, further complicating evolutionary scenarios that invoke a smooth, anagenic transition from one form to another.

Another intriguing detail was reported by Stringer (1993), who found that these "late archaic" or "intermediate" fossils from Africa are, in terms of their cranial metrics, strikingly similar to the Chinese specimens of Maba and Dali (and likely also Jinniushan, although Stringer did not have measurements for this specimen). Stringer (1993) noted that the phenetic similarity between his samples of African and East Asian late archaic humans was so close that it resembled the distance between geographically widely separated groups of humans in Howells's data set (Howells, 1973, 1989, 1995, 1996).

Florisbad

Florisbad consists of a partial cranium consisting of the face, the right M³, and much of the anterior portions of the cranial vault. It was discovered in 1932 in a fossiliferous spring eye in the Orange Free State, South Africa. The cranium was initially described by Dreyer (1935) as the type specimen of a new species, *Homo helmei*. Subsequent descriptions of Florisbad noted that it shared more features with modern humans than did Kabwe. These traits include a shorter face, canine fossa, and incipient division of each half of the supraorbital torus into supraorbital and superciliary segments (Drennan, 1935; Galloway, 1937; Keith, 1938). More recent descriptions largely agree, recognizing the cranium as intermediate in morphology between modern humans and archaic crania like Kabwe (Rightmire, 1978a, 1984a; Clarke, 1985). The cranium bears a canine toothmark on its frontal and may have been killed or scavenged by a large carnivore (Tappen, 1987). Curnoe and Brink (2010) have described other changes in the cranium, including lesions on the orbital roof and areas of thinning of the otherwise thick cranial vault, that indicate the individual had suffered from a pathology of indeterminate cause. Kappelman (1996) predicted a body mass of approximately 96kg for Florisbad based on its orbital area.

Early attempts to date sediments associated with the Florisbad cranium produced dates of 41–37 ka (Day, 1986); Protsch (1974, 1975) reported a direct ¹⁴C date of the cranium of 38–39 ka. These ¹⁴C dates should be read as infinite instead, as Vogel surmised (Day, 1986). More recently, Grün et al. (1996) obtained an ESR date from the hominin's tooth enamel of 259 ± 35 ka.

Additional studies of the locality include recent work on the site's vertebrate paleontology and archaeology (Brink and Henderson, 2001), as well as a brief report on Erfkroon, a contemporary fossil vertebrate locality in the Orange Free State (Churchill et al., 2000).

Eliye Springs (KNM-ES 11693)

The cranium from Eliye Springs was discovered by Dr. and Mrs. Darnhofer, who spotted its dark, round occipital protruding from the sediment while they were walking along a beach on the western shore of Lake Turkana (Bräuer and Leakey, 1986a). The cranium likely eroded by wave action from a nearby deposit bearing later Pleistocene fauna, but, unfortunately, its original provenience is unknown. It was originally described by Bräuer and Leakey (1986a, 1986b), who emphasized its affinities with other specimens of African late archaic *H. sapiens*. The cranium is heavily mineralized, stained very dark brown, and very well preserved except for the anterior portions of the supraorbital torus and face, which have been abraded. The cranial vault is long, low, and quite broad, with a rounded occipital, a greatest breadth of the cranium situated across the supramastoid crests, pronounced bossing on the parietals, a more vertical forehead than Kabwe or Bodo but not as vertical as in modern humans, and a broad but vertically short face.

Examination of the gross morphology of the cranial vault coupled with CT scans demonstrated that much of the cranial vault of KNM-ES 11693 is pathologically thickened to as much as 20.1 mm in the posterior portions of the parietal, 14 mm at lambda, and 16 mm at the temporal lines (Bräuer et al., 2003). The external surface of the vault also shows marked porosity, leading to the conclusion that the individual probably suffered from anemia from childhood onward (Bräuer et al., 2003).

Although the inside of the cranium of Eliye Springs remains filled with consolidated sediment, CT scans have permitted a study of the details of the virtual anatomy of the specimen's endocranial surfaces (Bräuer et al., 2004). The digital reconstruction showed that the endocranial capacity is approximately 1,210 cc (with a range between 1,170 and 1,245 cc). The anterior cranial fossa is relatively small, and the middle cranial fossa is at the shorter end of the few recent humans used for comparison. Otherwise, almost all of thirty-five endocranial features studied by Bräuer et al. (2004) fell within, or close to, the modern range of variation. The cranial base, however, is even more strongly flexed than in modern humans.

KNM-ER 3884

The partial cranium of KNM-ER 3884 was collected from the former Guomde Formation, which now has been divided between the underlying Chari and overlying Galana Boi formation (Feibel et al., 1989) in Ileret, East Turkana. It consists of the posterior parts of the cranium (occipital and fragments of the parietals), the frontal bone, and the palate and maxillary dentition (Bräuer et al., 1992a). It resembles other late archaic specimens like LH 18, Jebel Irhoud 1 and 2, Florisbad, and Omo II in various features, including a large cranial capacity, estimated at ~1,400 cc from the occipital's dimensions, which align the cranium with these late archaic specimens and show that it possessed some but not all of the apomorphies of later anatomically modern humans (Bräuer et al., 1992a; Bräuer, 2001b, 2008). Bräuer et al. (1997) reported a direct date on the fossil of 272 ka (range: 159 ka to infinity) to 279 ka (range: 162 ka to infinity) by $^{234}\text{U}/^{230}\text{Th}$ gamma ray spectrometry.

KNM-ER 999

A second specimen recovered from the formerly recognized Guomde Formation at Ileret in East Turkana, KNM-ER 999 consists of most of a left femur (Day and Leakey, 1973).

Trinkaus (1993) provided further analysis of the specimen, noting that it had a high neck-shaft angle like some of the Qafzeh and Skhul hominins, a distinct pilaster, and a point of minimum breadth located high on the shaft. All of these features resemble traits present in early modern and later hominins rather than *H. erectus* or archaic hominins like Neandertals, leading Trinkaus to argue that KNM-ER 999 showed affinities to modern humans. Bräuer et al. (1997) reported an absolute, direct date of the fossil of 301 ka (range: 205 ka to infinity) by $^{234}\text{U}/^{230}\text{Th}$ gamma ray spectrometry.

Ngaloba (Laetoli 18)

The Ngaloba cranium (also designated Laetoli Hominid 18 [LH 18]) comprises a calvaria and partial face (palate and maxillae). Collected in 1976 by Mary Leakey and her co-workers, LH 18 derives from the Ngaloba Beds at Laetoli, which also contain MSA tools (Day et al., 1980). Its anatomy, including a vertically short face, high vault, greatest cranial breadth located fairly high on the parietals, strong parietal bossing, small and medio-laterally narrow mastoid processes, and rounded occipital lacking a strong torus, clearly link the cranium with modern humans; only the receding forehead and large browridges indicate archaic affinities (Day et al., 1980; Magori and Day, 1983a, 1983b). The architecture of the cranial vault corresponds to the cranial “globularity” described by Lieberman et al. (2002) as a key morphological change that, along with facial retraction (Lieberman, 1998, 2008), produced modern cranial morphology.

The initial estimate of the age of LH 18 was approximately 120 ± 30 ka based on correlation with the trachytic marker tuff in the lower unit of the Ndutu Beds at Olduvai (Day, 1986). In an effort to clarify the age of the Ngaloba Beds and LH 18, Manega collected a series of ostrich eggshell fragments from the Upper Ngaloba Beds that contained the hominin. Amino acid racemization analysis (D/L ratio) of these suggested a minimum age of 205 ± 17 ka or 290 ± 25 ka for LH 18, after applying appropriate controls and adjustments for paleotemperatures (Manega, 1993). Subsequent summaries of hominin evolution (e.g., Bräuer, 2008) have tended to emphasize the younger revised age (~200 ka), but the cranium could well be older. Either way, Manega’s (1993) results provide another indication that hominins with nearly modern morphology lived in East Africa between 300 and 200 ka.

CT scans of Ngaloba are available from the Digital Archive of Fossil Hominoids of the Department of Anthropology at the University of Vienna.

Eyasi Remains

Continued work around Lake Eyasi in Tanzania (Mehlman, 1987; Domínguez-Rodrigo et al., 2007) has added to the fragmentary Eyasi cranium, occipital of a second individual, and vault fragments and teeth from a third (L. Leakey, 1936, 1946; Bräuer, 1984b). The new specimens include fragments of two mandibles and an occipital (Bräuer and Mabulla, 1996) and a frontal bone (Domínguez-Rodrigo et al., 2008). Trinkaus (2004) observed that the occipital of Eyasi 1 bears a suprainiac fossa, a feature usually associated with European hominins. Domínguez-Rodrigo et al. (2008) reported ESR (104 ± 13 to 207 ± 26 ka) and $^{230}\text{Th}/^{234}\text{U}$ (92.4 ± 4.1 to 138.3 ± 0.7 ka) ages for a wildebeest tooth found 5 m away from the new frontal.

Omo II

Since its initial description by Day (1969), the archaic affinities of the Omo II cranium have consistently been emphasized (Day and Stringer, 1982, 1991; Rightmire, 1984a; Bräuer, 1984b; Schwartz and Tattersall, 2003). Nevertheless, Day (1969) reported an estimate of the cranial capacity as $1,435 \pm 20$ cc. Most of the preserved basicranial details of Omo II recall

the anatomy of *Homo erectus*, and Stringer (1974) found that it clustered with Ngandong in multivariate space. However, the specimen has the same geological antiquity as Omo I (see below).

Jebel Irhoud Remains

Discoveries from Jebel Irhoud in Morocco consist of two adult crania and a juvenile humerus and mandible (Ennouchi, 1962, 1968; Holloway, 1981; Hublin and Tillier, 1981; Hublin et al., 1987; Hublin, 1992; Grün and Stringer, 1991; Grimaud-Hervé, 2005). Debate has swirled around possible Neandertal affinities of the crania; they certainly have long, low, and broad vaults, but the resemblance ends there. They have none of the apomorphic features that characterize Neandertals (Santa Luca, 1978; Hublin, 1992). Controversy also surrounds the degree of development of the chin on the juvenile mandible (Jebel Irhoud 3): Hublin et al. (1987) argued it has all of the components of a modern chin but weakly expressed on a vertical symphysis; other commenters have stated it does not bear a modern chin (e.g., Schwartz and Tattersall, 2000, 2003, 2010). T. Smith et al. (2007) reported an ESR and uranium-series date of 160 ± 16 ka for the site and also demonstrated that Jebel Irhoud 3 had a slow, fully modern pattern of dental development.

Earliest Modern Humans

Omo I

The partial skull and skeleton of Omo I was initially described as anatomically modern by Day (1969). Subsequent analysis supported Day's assessment (Day and Stringer, 1982, 1991; Day et al., 1991) and emphasized the differences with Omo II, which also derived from Member I of the Kibish Formation. The initial age estimate was of 130 ka based on a $^{230}\text{Th}/^{234}\text{U}$ date on a bed of Nile oyster shells in Member I and two ^{14}C dates on the same bed of greater than 39 ka (i.e., potentially infinite) (Butzer et al., 1969). At the time, Butzer et al. (1969) expressed caution about the $^{230}\text{Th}/^{234}\text{U}$ date, because it was known that uranium was water-soluble and could move in or out of deposits depending upon precipitation and the level of the water table; the effects of these uncertainties on mollusk shells had not been established. Although uncertainty over the antiquity of the specimen became a mainstay of multiregionalists' criticism of Omo I (see Fleagle et al., 2008), virtually all accepted that its cranial morphology was modern, or nearly so (although see Bartsiokas [2002] on Omo I's relatively thin layer of diploë in its cranial vault). Omo II, however, differed from modern humans in almost every preserved nuchal and basicranial detail, instead resembling *Homo erectus* (Day, 1969). This prompted Day to surmise that Omo II might be of greater geological antiquity, and many researchers have adopted a similar perspective. Renewed research in the Kibish Formation has pinpointed the find-spots of both Omo I and II. Both of these crania clearly derive from Member I, are underlain by the Nakaa'kire Tuff (dated to 196 ± 2 ka by $^{40}\text{Ar}/^{39}\text{Ar}$) low in Member I of the Kibish Formation and constrained in age by the Aliyo Tuff (dated to 104 ± 1 ka by $^{40}\text{Ar}/^{39}\text{Ar}$) near the middle of Member III, and approximately 24 meters above the level of KHS, the site where Omo 1 was discovered (McDougall et al., 2005, 2008; Brown and Fuller, 2008). Deposition of sediments in the lower Omo Valley appears to be closely linked to the amount of precipitation that falls on Ethiopia and thus also appears to correlate with sapropel deposition in marine sediments in the eastern Mediterranean. It seems likely that Member I of the Kibish Formation correlates with sapropel S7 (~195), Member II with sapropel S5 (~172 ka), Member III with sapropel S4 (~124 ka), and Member IV with sapropel S1 (~8 ka) (McDougall et al., 2005, 2008; Brown

and Fuller, 2008). Each sapropel accumulated fairly rapidly (at least in geological terms), over a span of approximately 10 ka, which corresponds to the spread of radiocarbon ages (13.1–3.6 ka) for Member IV atop the Kibish Formation (Brown and Fuller, 2008; McDougall et al., 2008). Given these facts, the best age estimate for Omo I, II, and the other hominins from Member I is 195 ± 5 ka.

There is no taphonomic or stratigraphic evidence to support assertions that Omo I is intrusive into Member I or that Omo II had been transported or eroded from older sediments and redeposited in Member I (Fleagle et al., 2008; Brown and Fuller, 2008; McDougall et al., 2008).

The renewed work in the Kibish Formation identified the find-spot of Omo I and led to the recovery of additional hominin remains at the site including two fragments of the left os coxae, the right talus, a fragment of the distal right femoral diaphysis that refits with the femoral condyles collected in 1967, and two right manual phalanges (Pearson et al., 2008a). Measurements of the acetabulum and humeral head predict a vertical diameter of the femoral head of 47.28 ± 1.24 mm, which implies a body mass of 70.73 ± 5.14 kg; height estimates range from 162.4 ± 5.1 cm to 172.3 ± 6.5 cm based on the length of the right metatarsal to 178.2 ± 4.25 cm to 182.3 ± 4.43 cm for the partial left humerus (Pearson et al., 2008a). The new fragments of os coxae provide a perplexing set of indications of sex including a large acetabulum (male), a greater sciatic notch shape that is intermediate between males and females, and the presence of a pre-auricular sulcus (female). It is possible that the pattern of sexual dimorphism at this point in human evolution differed from that of living humans, as Bonmatí et al. (2010) have documented for the Sima de los Huesos pelvis. Voisin (2008) concluded that Omo I's left clavicular morphology aligns it with living and Upper Paleolithic humans rather than Neandertals or earlier forms of *Homo*.

Work at other sites in the Kibish Formation produced additional finds, including a diaphysis and distal epiphysis of a left tibia (Kib 158-1a, from site AHS in Member I) and a piece of the diaphysis of a left fibula (Kib 158-1b) from the same site (and possibly from the same individual) and two cranial vault fragments (a posterior portion of an adult's right parietal [Kib 170-1] and a fragment of a juvenile's occipital [Kib 170-4]) from CHS, a site near the junction of Member III and IV, with an uncertain date (~8.6–104 ka) (Pearson et al., 2008b; Brown and Fuller, 2008).

If Omo I dates to 195 ± 5 ka, it would be older than most likely genetic dates for the origin of modern humans such as Fagundes et al.'s (2007) estimate of a speciation date of 141,455 BP (95% posterior probability density interval of 103,535–185,642 BP). Fagundes et al. (2007) derived this estimate from the best-fitting model of the origin and spread of modern humans to East Asia and the New World, a complete replacement of archaic Eurasians by African immigrants followed by exponential growth of the immigrants later in time. If the simulation approach and approximate Bayesian computation that Fagundes et al. (2007) used to explore the likely outcomes of complex demographic histories provide a reasonable approximation of reality, an age of ~141 ka for the origin of modern humans as a genetically distinct species has at least two interesting implications for the fossil record. There is reason to expect the ~141 ka date is reasonable: the values it derives from nuclear DNA polymorphisms in fifty loci resemble dates from mtDNA and Y chromosomes for the exodus from Africa and the settlement of the New World. Two implications for the fossil record are, first, that individuals whose morphology can be identified as “anatomically modern” appeared *before* the species originated, antedating it by ~50,000 years. Second, the date reinforces the impression from mtDNA (and human Y chromosomes with a coalescent age of 141.5 ± 15.6 ka [Cruciani et al., 2011]) that one or more events during MIS 6 (195–128 ka), a period of very low sea level and a massive glacial advance (the Riss Glaciation) in Europe, led to the origin of the genes that make up ~90–100% of the genotype of every living member of *Homo sapiens* (Green et al., 2010; Reich et al., 2010).

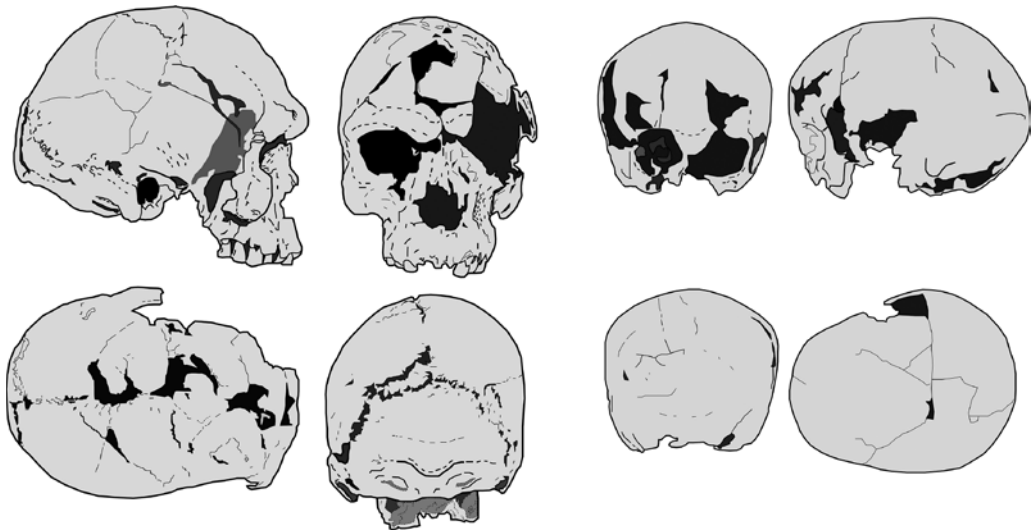


Figure 1.4. The best-preserved crania from Herto, scaled to the same size (after photographs by David Brill in White et al., 2003). Left: four views of BOU-VP-16/1, a strikingly large male cranium. Right: four views of BOU-VP-16/5, a cranium of a 6- to 7-year-old child.

Herto

White et al. (2003) described one juvenile and two adult crania from Herto in the Middle Awash, Ethiopia (Figure 1.4). Craniodental fragments of seven other individuals were reported in 2003, and the sample has now grown to fragments from a minimum of twelve individuals (White, 2009). All three of the most complete crania are arguably anatomically modern, or nearly so, but very robust. The best preserved cranium, BOU-VP-16/1 is easily distinguished from living humans, in part by its size alone given its glabella-opisthocranium length of 219.5 ± 2 mm and its nasion-prosthion length of 79 ± 3 (White et al., 2003). To put these values in perspective, the longest of the 2,524 crania in Howells's online data has a glabella-opisthocranium length of 206 mm, and only 30 individuals have a nasion-prosthion length of 79 mm or greater. The proportions and morphological traits of the Herto crania, however, match the expectations for a modern human (e.g., Day and Stringer, 1982, 1991; Stringer, 2003), leading White et al. (2003) to propose the subspecific designation of *Homo sapiens idaltu* for the Herto specimens. The crania have a high cranial vault, a widest point of the cranium located high on the parietals (which give them an *en maison* shape in posterior view), a more obtuse angle between the upper and lower tables of the occipital than in *H. erectus*, higher frontal angle, a modern cranial capacity (1,450 cc for BOU-VP-15/1 and 1,250 cc for BOU-VP-15/5), a distinct canine fossa, a supraorbital torus divided by a sulcus into a thick supraorbital segment and a thinner superciliary segment, medio-laterally narrow mastoid processes, and a face that appears to be retracted beneath the frontal bone (White et al., 2003). The child's cranium differs from the adult in being substantially smaller (especially with respect to maximum length) and has minimal development of its supra-orbital torus, and a much less projecting mastoid process and a smaller face, as one might expect in a juvenile. It also has very well-developed parietal bosses and a much more rounded contour of the external surface of the occipital. These details combine to endow BOU-VP-15/5 with an unequivocally modern morphology.

The crania were found in association with a stone tool industry that has handaxes as well as MSA components, and all three crania bear peri-mortem cutmarks likely made by a stone

tool (Clark et al., 2003). The sediments that yielded the crania have been precisely assigned to the interval between 160 and 154 ka by $^{40}\text{Ar}/^{39}\text{Ar}$ dating of over- and underlying tuffs (Clark et al., 2003).

Singa

The cranium from Singa was collected from the bank of the Blue Nile in Sudan about 320 km south of Khartoum. It was initially described as an ancestral Bushman by Woodward (1938) on the basis of its pronounced parietal bosses and strongly developed browridges. A later analysis by Stringer et al. (1985) noted that the exaggerated parietal bosses may stem from pathology. Its browridge is reduced in size versus Kabwe, Bodo, and even Florisbad but still prominent compared to most living Africans. Singa features a high cranial vault, fairly vertical forehead, and a rounded occipital. Stringer (1979) applied a multivariate analysis of Penrose distances to Singa and a set of other recent and fossil crania and found that no other Pleistocene cranium provided was especially close to it. Jebel Irhoud 1 lay closest to Singa in Penrose space, leading Stringer (1979) to conclude that the specimen's affinities lay with African late archaic specimens like Jebel Irhoud.

Removal of the matrix filling the cranium and preparation of an endocast allowed the specimen's cranial capacity to be ascertained to be 1,340 cc (Stringer et al., 1985). McDermott et al. (1996) obtained a U/Th date for the cranium of $> 133 \pm 2$ ka on calcrete matrix inside the cranium, placing it near the end of MIS 6. Although the overall morphology of the Singa cranium differs from what one would expect in a modern human, the U/Th dates suggest it is substantially more recent than the earliest examples of anatomically modern (or nearly modern) Herto crania and Omo I.

Aduma

Haile-Selassie et al. (2004) described four partial crania from Aduma (ADU-VP-1/1, ADU-VP-1/2, ADU-VP-1/3, and ADU-VP-1/6) and a right parietal from Bouri (BOU-VP-5/1) in the Middle Awash research area in Ethiopia. The best preserved cranium, ADU-VP-1/3, bears a suprainiac fossa on its occipital but otherwise is modern in form, resembling those of Omo I, LH 18, Skhül V, and Qafzeh 9 (Haile-Selassie et al., 2004). The overall affinities of ADU-VP-1/3 clearly lie with early modern humans. The same appears to be the case for the long BOU-VP-5/1 parietal and, as far as can be gauged, the much more fragmentary remains of the other Aduma crania. The Aduma crania and Bouri parietal derive from sediments with sites bearing MSA tools and dating between 80 and 100 ka (Yellen et al., 2005). The tools recovered from Aduma represent a distinctive regional tradition defined by a range of point, scraper, and core types as well as tools of small, almost microlithic size (Yellen et al., 2005).

Klasies River (Klasies River Mouth)

Originally excavated by J. Wymer and R. Singer (Singer and Wymer, 1982) and later by H. Deacon (1989, 1992; Deacon and Geleijnse, 1988; Deacon and Shuurman, 1992), the site of Klasies River has figured prominently in the debate over the origin of modern humans for two reasons. First, it yielded a series of human remains, which are rarely recovered from MSA contexts in southern Africa, that had modern morphological affinities and that, by the early 1980s, had a suggested antiquity of around 100 ka (Butzer, 1978; Volman, 1978; Singer and Wymer, 1982). Later work to obtain ESR dates for the site has confirmed this antiquity,

placing all of the hominins from the MSA within the time span of 60–120 ka, with most centering around 100 ka (Grün et al., 1990b; Deacon and Shuurman, 1992). Second, the degree to which the hominin fossils were anatomically modern or not became the subject of debate throughout the 1990s. Arguments against the anatomical modernity of the specimens generally occurred in the context of multiregionalists' attempts to argue that fossils of modern humans had not appeared earlier in Africa than elsewhere (e.g., Wolpoff, 1989; F. Smith, 1992, 1993, 1994; Smith et al., 1989; Frayer et al., 1993). Although the hypothesis that modern humans did not make an early appearance in Africa has been disproven (White et al., 2003; McDougall et al., 2005), how to interpret the anatomy of the hominins from Klasies River remains an interesting issue.

The initial sample of hominin remains from the MSA levels at Klasies River (Singer and Wymer, 1982) has been augmented by recent finds and now comprises five partial mandibles, a frontal bone, a left zygomatic, two maxillary fragments from the LBS Member (Bräuer et al., 1992b), at least ten isolated teeth (Rightmire and Deacon, 2001), a small part of a left os coxae, temporal (Grine et al., 1998), the proximal end of a right radius (Pearson and Grine, 1997), a proximal left ulna (Rightmire and Deacon, 1991), a partial atlas (Grine et al., 1998), a lumbar vertebra, a left metatarsal I, a very long left metatarsal II, and a more moderately sized right metatarsal V (Rightmire et al., 2006a). Singer and Wymer's (1982) description of the hominins from the MSA levels at Klasies River emphasized the modern affinities of the material, although they noted that some of the mandibles had minimal development of a chin and that there was a considerable amount of size variation in the height of the mandibular corpus and molar dimensions. Additional analysis of this material showed that some of the cranial remains appear to have been defleshed by humans wielding stone tools that left cutmarks on the bones (White, 1987). Metrical analysis of the ulna showed it to have a comparatively low coronoid process that aligned it with many archaic humans including Neandertals and the KNM-BK 66 ulna (Churchill et al., 1996).

Controversy regarding the Klasies material sprang from claims that the modern morphological affinities of the material had not been clearly established. F. Smith (1992, 1993, 1994) and Frayer et al. (1993) emphasized that the degree of development of the chin on many of the mandibles was, in fact, weak (or even absent); the late Neandertals from Vindija in Croatia could be considered, they argued, to have a similar degree of chin development. Lam et al. (1996) reassessed the external midsagittal profiles of the mandibles, concluding that each chin that could be evaluated fell within the 95% envelope of variability for modern humans but that it was unlikely that a sample of more recent humans would produce such a high proportion of individuals with weakly developed chins. Lam et al. also noted that the variation in size between corpus dimensions at M_1 of the mandibles KRM 16424 and KRM 13400 would be unlikely ($p < 0.05$) to be encountered in a sample of recent humans. The same applies to the tiny size of the molars of KNM 16424. Royer et al. (2009) performed a more complex resampling study of the molar and mandibular corpus dimensions of the Klasies specimens and confirmed that they showed elevated variability compared to samples of recent humans, but that hominins from Skhül, Dolní Věstonice, and Sima de los Huesos also showed elevated variability, although Neandertals did not. A second argument focused on the Klasies zygomatic bone, which is vertically high, implying a tall face, and has a thick, column-like frontal process that is characteristic of archaic humans (Wolpoff, 1992; Wolpoff and Caspari, 1990, 1996; F. Smith, 1992, 1994). Among modern humans, however, both of these morphological details are variable and the Klasies specimen's morphology does not exclude it from the modern range of variation (Bräuer and Singer, 1996a, 1996b). The debate continues; Cartmill and Smith (2009) have reiterated their view of the archaic affinities of the Klasies zygomatic.

Border Cave

The hominin fossils, especially the cranium (Cooke et al., 1945; de Villiers, 1973; Rightmire, 1979, 1981) and mandibles (de Villiers, 1973, 1976) from Border Cave, played a large role in the debate over the origin of modern humans due to early and successful efforts to establish the antiquity of the MSA deposits at the site (Klein, 1977; Butzer et al., 1978; Beaumont et al., 1978; Beaumont, 1980) and the obviously modern morphological affinities of the cranium and mandibles (de Villiers, 1973, 1976; Rightmire, 1979, 1981, 1984a; Bräuer, 1984b).

Fossils from Border Cave that have been described since the 1980s comprise a fragment of a right humeral diaphysis, proximal right ulna, and right metatarsals IV and V, lacking their heads (Morris, 1992). The humerus was later evaluated by Pfeiffer and Zehr (1996) and Pearson and Grine (1996), and the ulna by Pearson and Grine (1996). The ulna has a relatively low coronoid process like the Klasies River specimen (Churchill et al., 1996). Sillen and Morris (1996) measured bone mineral crystallinity via infrared spectroscopy in fauna from Border Cave as well as the ulna, humerus, and the two mandibles from the MSA. Their results showed that the ulna and humerus matched the MSA-derived fauna in crystallinity, but the mandibles did not and thus might be of recent date rather than ~90 ka. However, a more recent ESR and laser ablation study of an enamel chip from the Border Cave 5 mandible (Grün et al., 2003) placed the specimen at 74 ± 5 ka, which indicates it derives from the MSA, although it is of a more recent age than it had appeared to be in the 1990s.

Other MSA sites in South Africa have yielded a few hominin fossils. These include isolated hominin fragments, primarily teeth, from the sites of Die Kelders (Grine et al., 1991; Grine, 1998, 2000), Blombos (Grine et al., 2000; Grine and Henshilwood, 2002), Equus Cave (Grine and Klein, 1985), Sea Harvest (Grine and Klein, 1993), and Witkrans (McCrossin, 1992). The teeth tend to be large relative to the recent inhabitants of southern Africa, although a few specimens are smaller like the M² from Witkrans (McCrossin, 1992). The record for additional postcranial remains is even sparser. Grine and Klein (1993) described a slender distal manual phalanx from the MSA levels of Sea Harvest. The site of Blind River produced a left femoral diaphysis lacking the proximal end that was originally reported and described in the 1930s (Laidler, 1933; Wells, 1935); Wang et al. (2008) have reanalyzed the specimen and reported OSL and geological dates that indicate that the sediments that contained the femur began to accumulate immediately following the period of high sea level during MIS 5e.

The only other fossil that might derive from the MSA in Southern Africa is Oranjemund, a calvaria from terrace deposits near the mouth of the Orange River in southern Namibia (Senut et al., 2000). It has a relatively low vault, receding frontal bone, and moderately strongly developed browridges. It is, unfortunately, effectively undated at present.

Hominins from the Late MSA or Early LSA

Hofmeyr

The partial skull from Hofmeyr is an important specimen for understanding the later stages of human evolution in southern Africa. The cranium was originally discovered in 1952 in a dry bed of the Vlekpoort River in the Eastern Cape Province of South Africa, but languished in obscurity because its antiquity could not be established. An attempt to obtain a radiocarbon date in the 1960s sacrificed a large part of the left parietal to no avail because no date was published; another smaller piece was submitted for AMS dating at Oxford in the 2000s but lacked enough collagen to obtain a date (Grine et al., 2007). Instead, sediments in the endocranium of Hofmeyr were dated to 36 ± 3.3 ka through a combination

of OSL and uranium-series dating (Grine et al., 2007). This age establishes the cranium as one of the very few specimens from South Africa from the period between the earliest fossils of modern humans in the region at ~100 ka and the Holocene population.

Grine et al. (2007) noted that the cranium displays a number of primitive traits in comparison to more recent African crania including large molar crowns, a prominent glabella and fairly thick, salient, and continuous browridges, and a high and flat zygomatic bone with a thick frontal process. Metrically, however, after Procrustes superimposition of 3D landmarks on the cranium, Hofmeyr falls among a variety of recent populations in a canonical variates analysis, and, intriguingly, falls closest of all to the mean of the Upper Paleolithic European crania included in the analysis (Grine et al., 2007). This fact suggests the cranium represents a relatively undifferentiated specimen of early modern humanity and corroborates the view that most of the morphological differences that distinguish geographically separate populations of modern humans developed only within the last 36 ka (de Villiers and Fatti, 1982; Stringer and Andrews, 1988; Habgood, 1989; Howells, 1989, 1995; Lahr, 1996). Grine et al. (2010) have presented a geometric-morphometrics-based reconstruction of missing portions of Hofmeyr and, using the reconstruction, estimated the endocranial capacity to be $1,580 \pm 2.7$ cc.

Outside of South Africa, a number of other finds document human evolution through the later MSA, including Mumbwa in Zambia, Mumba in Tanzania, Porc-Épic in Ethiopia, Taramsa Hill and Nazlet Khater 2 in Egypt, and Dar-es-Soltane 5.

Mumbwa

The site of Mumbwa in Zambia was excavated by Del Grande (Dart and Del Grande, 1931) and Desmond Clark (Clark, 1942), followed by renewed work by Barham (1995, 1997, 2000). Barham's expedition uncovered traces of the use of red ochre from MSA levels at Mumbwa as well as from the late Acheulean site of Twin Rivers (Barham, 1998). Barham also uncovered a number of new hominin specimens from the MSA (or possibly from the MSA), including three molars or molar fragments, a left femoral diaphysis, and a proximal and distal fragment of a right radius (Pearson et al., 2000), as well as a small fragment of a hominin humerus from Twin Rivers (Pearson, 2000).

Mumba

Mehlman's (1989) excavation of Mumba Cave in Tanzania yielded two upper molars from the MSA layers. The teeth are notably small in comparison to homologous teeth from recent Africans (Bräuer and Mehlman, 1988). McBrearty and Brooks (2000) reported amino acid racemization on ostrich eggshell of 65–45 ka for Level V at Mumba, which contains the Mumba Industry (Mehlman, 1989). New excavations are under way at Mumba (Prendergast et al., 2007); hopefully additional dates for its MSA deposits will be forthcoming.

Porc-Épic (Diré-Dawa)

Early excavations at Porc-épic Cave near Diré Dawa, Ethiopia, produced a partial hominin mandible (Vallois, 1951) that likely belonged to an early modern human. Later excavations (Clark et al., 1984) recovered additional human craniodental fragments that were discovered while cleaning brecciated fauna from the site (Assefa, 2006) in preparation for study (Assefa, personal communication). Additional recent work from the site has analyzed the lithics (Pleurdeau, 2003, 2005) and uncovered a series of pierced gastropod opercula that were likely used as beads (Assefa et al., 2008).

Taramsa Hill

Excavations at Taramsa Hill near Qena in Upper Egypt, discovered a juvenile burial consisting of a skull and skeleton, of an approximately 8- to 10-year-old child who had been buried in a pit in a Middle Paleolithic chert quarry (Vermeersch et al., 1998). An additional stratum of Middle Paleolithic quarrying debris covered the grave and provided an initial guide to its antiquity. OSL dating sediments from Middle Paleolithic chert extraction pits associated with the skeleton yielded ages ranging from 49.8 to 80 ka, with a weighted average of 55.5 ± 3.7 ka (Vermeersch et al., 1998). Preliminary morphological observations based on excavation photographs show the teeth to be large, the cranium highly domed and gracile, and much of the bone of the mandible to have disintegrated. The skeleton remains in Egypt, awaiting conservation, excavation, and further study.

Nazlet Khater

Nazlet Khater is a skull and partial skeleton recovered from an Upper Paleolithic quarry in Upper Egypt (Vermeersch et al., 1984). The burial and the main flint mining at the quarry date to ~40–35 ka based on OSL and AMS ^{14}C dates (Crevecoeur, 2008). Nazlet Khater was initially described by Thoma (1984); subsequent studies have analyzed the mandible (Pinhasi and Semal, 2000), inner ear (Crevecoeur, 2007; Bouchneb and Crevecoeur, 2009); and, most recently, the entire skeleton (Crevecoeur, 2008) and comparative cranial morphology (Crevecoeur et al., 2009). The skeleton is of a young man, around 161 cm in stature, with a body mass of around 53.4 kg based on the size of his femoral head (Crevecoeur, 2008). The skull and postcranial skeleton show a number of primitive and idiosyncratic features but are modern in overall morphology (Crevecoeur, 2008). A recent analysis of three nearly contemporary crania, Nazlet Khater, Peștera cu Oase, and Hofmeyr, shows that they are surprisingly variable, more so than recent humans (Crevecoeur et al., 2009), a finding replicated in other studies (Gunz et al., 2009).

Dar-es-Soltane II

Dar-es-Soltane II, a cave in Morocco, contained the partial cranium and hemimandible of a strikingly robust adult male, Dar-es-Soltane 5, as well as an adolescent's mandible and the calvarium of another juvenile (Débenath, 1975, 1980; Ferembach, 1976). The hominin remains from the site date to the upper Aterian, which in the late 1980s appeared to date between 40 and 20 ka (Hublin, 1992). Recent work has established a much greater antiquity for the Aterian. Richter et al. (2010) have reported TL dates of 83.3 ± 7.8 and 145 ± 9 ka for two levels of Aterian artifacts from Ifri n'Ammar, Morocco, and Bouzouggar et al. (2007) announced OSL dates of 82 ka for Aterian levels containing pierced shell beads from the site of Grotte des Pigeons at Taforalt, Morocco. At Taforalt, the MP (Aterian) lasts into Bed C, dated by ^{14}C , OSL, and TL to at least 20.2–37.4 ka, although Upper Paleolithic tools make their first appearance at the top of the Bed C and the Aterian disappears (Bouzouggar et al., 2007).

Descriptions of Dar-es-Soltane 5 have emphasized its affinities to anatomically modern humans (Ferembach, 1976; Hublin, 1992), but it also has a heavily developed, strongly projecting browridge, a very broad face, interorbital distance, and cranial vault, and very large teeth (Hublin, 1992; Schwartz and Tattersall, 2003). The other Aterian hominin remains described so far, including a mandible and occipital from Temara and another mandible and an isolated canine from Zouhra Cave, are also anatomically modern but robust and megadont (Hublin, 1992).

Given the great antiquity of the Aterian in North Africa, if recent results from mtDNA of a spread across North Africa at 40–45 ka of people whose mtDNA is closely related to the oldest surviving lineages in Europe and the Near East (Olivieri et al., 2006) also reflects

what happened in the rest of the genome, then the Aterian inhabitants of the Maghreb contributed very little to the genetic heritage of the living population of the region. Instead, the evidence from mtDNA suggests that they were largely replaced, much like Neandertals in Western Europe, despite the evidence for their supposedly modern cognition in the form of shell beads (Bouzougar et al., 2007) and their anatomically modern morphology.

Haua Fteah

Two partial mandibles were recovered from MSA layers in the massive cave of Haua Fteah in Libya and described in the 1950s and 1960s as having Neandertal affinities (McBurney et al., 1953; Trevor and Wells, 1967; Tobias, 1967). Bräuer (1984b) concluded that this was more a product of the interpretive framework of the time in which Middle Paleolithic industries around the Mediterranean were automatically associated with Neandertals; the mandibles lack any Neandertal apomorphies and likely derive from early modern humans. Additional recent work has focused on analyses of old collections, including the fauna from the Middle Paleolithic levels (Klein and Scott, 1986) and the lithics (Chazan, 1995), and new excavations led by Graeme Barker of Cambridge University have been under way since 2007.

Hominins Formerly Thought to Date to the MSA

Fish Hoek 1

Fish Hoek 1, a well-preserved cranium and mandible, has long figured in discussions of the fossil record of southern Africa as a possible representative of the MSA population (e.g., Sampson, 1974). It was excavated between 1927 and 1929 by V. and B. Peers, amateur archaeologists, from the Howiesons Poort levels of Peers Cave (Skildergat) near the town of Fish Hoek on the Cape Peninsula, South Africa. Keith (1931) provided an initial description and illustrations of the cranium, noting that it generally resembled the skulls of modern Khoesan people but was larger in size. Recently, the controversy over the specimen's age was settled by direct AMS ¹⁴C dating, which showed the specimen dates to 7,457–7,145 cal BP (Stynder et al., 2009).

Tuinplaas

Tuinplaas (Springbok Flats) is a partial skull and skeleton (Toerien and Hughes, 1955; Hughes, 1990) from Gauteng Province, South Africa. Uranium-series dating by Pike et al. (2004) determined the skeleton's age to fall between 11.0 ± 0.7 and 20 ± 3 ka. These dates remove the skeleton from the MSA, but show that, if the skeleton provides a reasonable window on the population from which it came, the terminal Pleistocene inhabitants of northeastern South Africa were substantially taller and had larger cranial dimensions than the late Holocene San inhabitants of the area. If so, this would support the idea that a substantial amount of morphological change happened in the early Holocene human population in southern Africa.

Emergence of Distinctive Regional Groups in Africa

Curiously, although modern humans appeared very early in Africa, there was a very long delay until the appearance of individuals who can not be distinguished metrically and morphologically from the living inhabitants of each part of Africa. In fact, almost all Africa Late Pleistocene hominins are easily distinguished from living Africans (Anderson, 1968; Brothwell and Shaw, 1971; Gramly and Rightmire, 1973; Twiesselmann, 1991; Muteti et al., 2010;

Angel et al., 1980; de Villiers and Fatti, 1982; Angel and Olsen Kelly, 1986; Habgood, 1989; Howells, 1989; Boaz et al., 1990; Allsworth-Jones et al., 2010), and it is not until the Holocene that this situation changes (Rightmire, 1975, 1978b, 1984b; de Villiers and Fatti, 1982; Bräuer, 1984b; Habgood, 1989).

The Climatic Background

The 1990 view of the impact of climate that prevailed in the 1990s stressed the importance of Marine Oxygen Isotope Stages (or MIS) as a possible key for understanding the origin of modern humans. The first fossils of modern humans occurred in Africa between 200 and 150 ka (MIS 6) and had spread to Israel by at least 100 ka (MIS 5). This spread from Africa possibly occurred during MIS 5e, a warm and wet period of higher sea level than today between 127 and 115 ka. MIS 6, which corresponded to the Riss Glaciation in Europe and low sea levels worldwide, is intriguingly associated with the origin of modern humans. It is possible that a drier Africa would have supported a small and perhaps fragmented human population. Demographic contraction and isolation could have served as the trigger for the origin of modern humans, either by drift or selection (or perhaps both).

Recent work has produced a somewhat different view of what happened, especially during the last 100 ka in equatorial Africa. The new view stems largely from terrestrial records, especially cores from Rift Valley lakes, rather than the marine record. Cores from Lake Malawi show several periods of marked aridity between 135 and 75 ka, especially between 135 and 127 ka and 100 and 85 ka, with a dramatic rise in lake levels with the return of wetter conditions at around 70 ka and modern level by 60 ka (Scholz et al., 2007; Cohen et al., 2007), the approximate date of the exodus from Africa that led to the establishment of modern humans throughout Eurasia and beyond (Macaulay et al., 2005). These geological findings of megadroughts in the Late Pleistocene likely explain why there was such a long delay between the origin of modern morphology in Africa and the spread of modern people outside of the continent.

Speciation

Perhaps no other question has vexed anthropologists as much recently as the issue of how many hominin species lived in the Middle to Upper Pleistocene. Speciation may have occurred during the transition from *Homo erectus* to *Homo heidelbergensis* (or *Homo rhodesiensis* or *Homo antecessor*) (Rightmire, 1996; Stringer 2003). The range of opinion on the issue falls along a familiar spectrum from splitters to lumpers. On the extreme splitter side of the divide, Schwartz and Tattersall (2003) recognize a large number of “morphs,” presumably (or at least possibly) distinct species. Arsuaga’s (2010) recent overview of the place of the Sima de los Huesos material indicates he too is inclined to recognize a number of distinct populations of Middle to Upper Pleistocene fossils that could be designated as distinct species. Rightmire (1996, 1998, 2001a, 2001b, 2001c, 2008) favors the recognition of *H. erectus*, *H. heidelbergensis*, and two descendants of *H. heidelbergensis*, *H. sapiens* and *H. neanderthalensis*. Stringer (2003) follows suit but recognizes that *H. antecessor* or some other, earlier fossil may also have played a role as the ancestor of both modern humans and Neandertals, thereby complicating Rightmire’s phylogeny and possibly making *H. heidelbergensis* an exclusively European taxon and the African forms that resemble it *H. rhodesiensis*.

Lumpers adopt a seemingly simpler view of hominin diversity during the Middle to Upper Pleistocene, but, on closer inspection, their view contains all of the same morphological

complexity but assigns much or all of it to a lower taxonomic rank. A case in point is Bräuer's (1984a, 1984b, 2008) view that hominin species in Middle to Late Pleistocene Africa are all *Homo sapiens* from the Middle Pleistocene, (i.e., a single evolving lineage), divided into different grades (Figure 1.2). This scheme has, however, drawn criticism. F. Clark Howell (1994: 303–304) wrote:

The informal appellation, archaic *Homo sapiens*, which increasingly gained currency over the past quarter-century, has served more to obscure than to clarify aspects of hominid phylogeny. It, of course, implies attribution *both* to a particular species ((*H.*) *sapiens*) on the one hand, and simultaneously a grade within said species on the other hand. The latter is usually contrasted with “archaic modern” and “anatomically modern.” Thus, although the usage seemingly appears straightforward it is, in fact, informal: no basis for this practice exists within the International Code of Zoological Nomenclature. The term has no formal basis, and it has been applied almost wholesale to an extraordinary diversity of fossil hominid remains from Eurasia as well as Africa, which often differ substantively one from the other, and both spatially and temporally, it is frankly best abandoned altogether.

Howell's alternative to the unsatisfactorily vague term of “archaic *Homo sapiens*” was to place fossils in paleodemes (or “p-demes”), ostensibly members of potentially interbreeding populations in very close geographic and temporal proximity (Howell, 1994, 1999). Howell recognized that some paleodemes seemed clearly more similar to one another than to others, but in these late contributions, he was quite circumspect about specifying which ones constituted bona fide species.

The multiregional view, as championed by Milford Wolpoff, of Middle to Late Pleistocene species has always been much simpler than the schemes endorsed by splitters. Wolpoff's view (e.g., Wolpoff et al. 1984; Wolpoff, 1989, 1996; Frayer et al., 1993) is that there has only been one species of *Homo* since the appearance of what most researchers would term *H. erectus*, if not from even earlier. Wolpoff and his co-authors have made clear that they certainly recognize geographic and temporal variants within the species that they consider to be the products of selection and genetic drift. Despite the existence of these variants, Wolpoff and colleagues emphasize that those variants were of less importance than the overall coherence of the species, which was maintained by gene flow throughout the entire span of the Pleistocene. Wolpoff (1996) made logical extension of this argument by designating all of the members of the species as *Homo sapiens*, with the specimens many other researchers assign to *H. erectus* designated as early *Homo sapiens*.

A potentially useful alternative to endless debates over how many species one should recognize comes from de Queiroz's (1998) insight that speciation is a process, often a long one, and that the criteria that paleobiologists use to differentiate species (e.g., statistically significant differences in the means of metrical traits despite substantial overlap, a diagnosable morphological difference, reduced fitness of hybrids, a difference in the mate recognition system, hybrid infertility, no interbreeding that produces viable offspring, no interbreeding, or the appearance of many discrete morphological and genetic differences with no overlap in polymorphisms) all merely represent different criteria that will be eventually met the further two populations move along a pathway to complete separation and divergence. It is likely that de Queiroz's model applies to human evolution during the Middle to Late Pleistocene (Pearson, 2008), and that the divergences that can be observed between populations of hominins reflect the fact that they had moved part of the way along the path of speciation (Figures 1.5 and 1.6). Studies of baboon hybridization in Africa (Jolly, 2002) caution that the million or so years that are the subject of this chapter are almost certainly too little time to produce hybrid inviability (Holliday, 2003), and the recent revelations that approximately 1–4% of the genetic heritage of people outside of sub-Saharan Africa derive

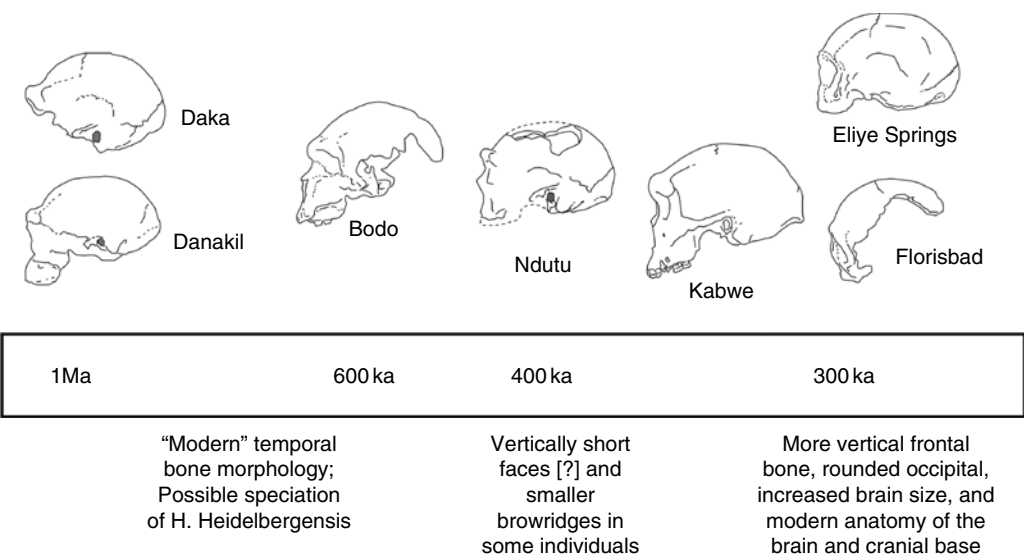


Figure 1.5. Sequence of cranial evolution in Africa, Part A (from Pearson, 2008).

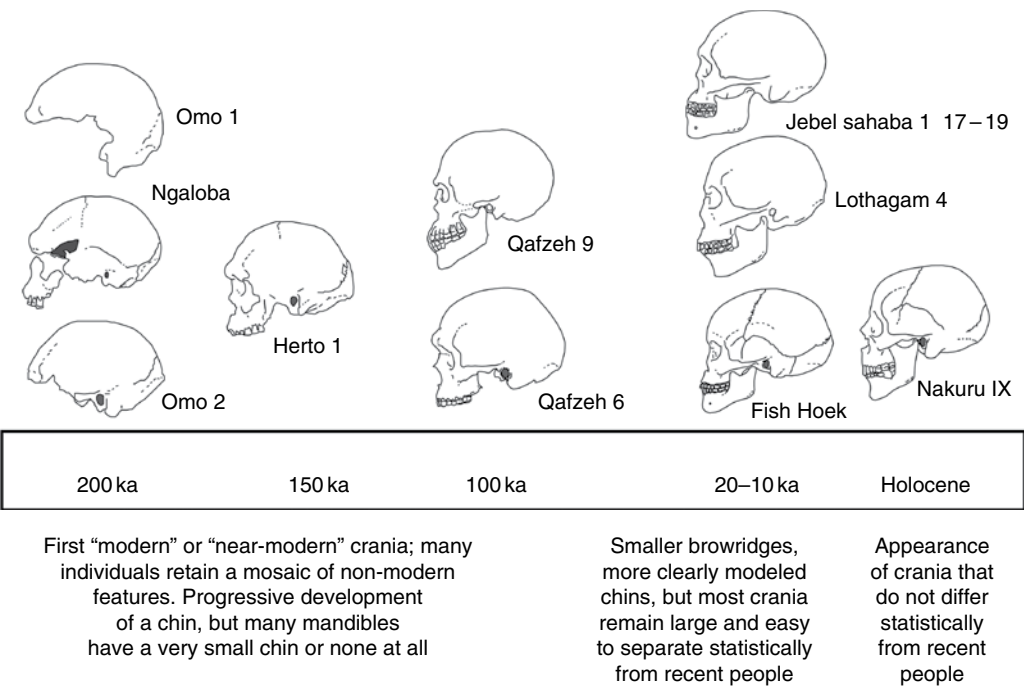


Figure 1.6. Sequence of cranial evolution in Africa, Part B (from Pearson, 2008).

from Neandertals (Green et al., 2010), and hominins like the “Denisovans” from Siberia contributed 4–8% of the genes present in Melanesians (Reich et al., 2010), indicate conclusively that interbreeding occurred at least occasionally between genetically (and almost certainly morphologically) distinct populations in the Pleistocene (Figure 1.7).

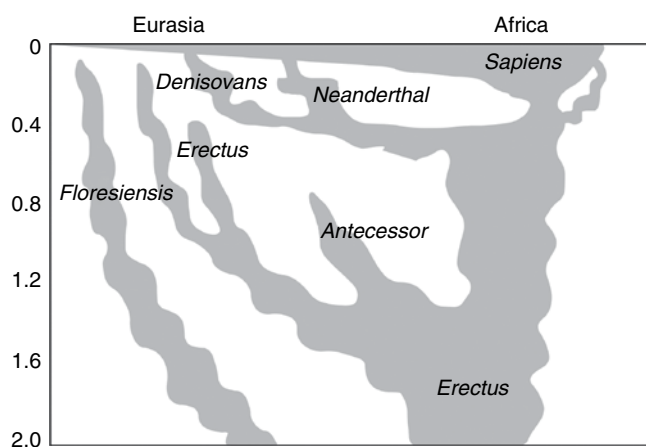


Figure 1.7. The latest phylogeny envisioned by Chris Stringer (after Stringer, 2011). The phylogeny incorporates reticulate evolution with Neandertals (Green et al., 2010), Denisovans (Reich et al., 2010), and archaic hominins within Africa (Wall et al., 2009; Hammer et al., 2011).

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Chapter 2

Crossroads of the Old World: Late Hominin Evolution in Western Asia

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While the origin(s) of modern humans (*Homo sapiens sensu stricto*) remains the oldest question in paleoanthropology, the last few years have finally brought a great deal of resolution to the question of our species' origin, a degree of resolution that was nearly unthinkable at the time of publication of the 1984 volume. It is now a near certainty that modern humans emerged first in East Africa ca. 200 ka and subsequently (and seemingly gradually) expanded to other parts of Africa and beyond in a scenario not unlike that hypothesized in the "Recent African Origin" (RAO, or "Out of Africa [II]") model. However, when these modern humans encountered non-modern hominins in other parts of the Old World, we now know from both morphological and genetic evidence that they interbred with those nonmodern hominins to produce viable, fertile offspring—not unlike the scenario(s) long posited by supporters of the "Multiregional Evolution (MRE)" or "Regional Continuity" model. Thus, as was first suggested by the early population genetic studies of extant human mitochondrial DNA (Cann et al., 1987; Vigilant et al., 1991), the majority of human genes today are derived from that original East African founding population, but unlike the scenarios posited in those early papers, in extant non-African humans these genes are complemented by those contributed by Neandertals and other non-African forms of archaic *Homo* (Green et al., 2010; Reich et al., 2010). In this light, the question of whether today's view of modern human origins is a revised RAO or a modified MRE model is really a semantic issue. In fact, it is more appropriate to acknowledge that intermediate models, based entirely on paleontological data, such as Smith's "Assimilation" model (Smith, 1984, 1992, 1994; Trinkaus, 1986; Smith et al., 1989; Smith and Trinkaus, 1991), or the "African Origin and Hybridization" model of Bräuer (Bräuer, 1984, 1989, 1992, 2008), in the end had provided the most accurate picture of the pattern of modern human origins as it is currently understood. In modern human origins, at least, what remain unresolved are nuances to a well-documented overall pattern.

As modern humans began to expand beyond Africa in the Middle and Late Pleistocene, likely the first area into which they expanded was Southwestern Asia, strategically located at the "crossroads" of the Old World between Europe, Africa, and Asia. The route(s) through which these humans expanded beyond Africa is either across the Sinai Peninsula

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and into the Levant, or alternatively across the Bab al-Mandab Strait between the Horn of Africa and the Southwestern Arabian Peninsula, or both (Lahr and Foley, 1998; Armitage et al., 2011). Western Asia therefore plays a critical role in our understanding of modern human origins, since it is the corridor through which modern humans moved into Europe and East Asia and is argued by some (Green et al., 2010) to be the area in which most of the gene flow between these expanding modern human populations and Neandertals occurred. Western Asia has also long provided the most extensive and informative sample of human skeletal remains relevant to this dynamic. Within Western Asia, Pleistocene *Homo* is known from Israel, Lebanon, Syria, Iraq, Iran, and Georgia, while in West-Central Asia, Late Pleistocene hominin fossils have thus far been uncovered in Uzbekistan, Tajikistan, and Siberia.

In the years since the publication of the 1984 volume, there have been multiple fossil hominin discoveries, as well as reinterpretation of some of the existing fossils from Western and West-Central Asia. This chapter will serve as a review of the current state of knowledge of Late Pleistocene hominins in Western (and West-Central) Asia, primarily through the lens of how they relate to the emergence of modern humans as a process now known to have included both exogenous gene flow from Africa with a smaller (yet significant) genetic input from local non-modern forms of the genus *Homo* outside of Africa (Templeton, 2002, 2005; Evans et al., 2006; Green et al., 2010; Reich et al., 2010).

Late Pleistocene Western Asia: Anatomical and Taxonomic Variability

Since the first anatomical description of the hominin fossils unearthed by Dorothy Garrod's team from the Mount Carmel caves (in particular those from Mughareh et-Tabun ["Cave of the Oven"] and Mughareh es-Skhul ["Cave of the Children"]) in the 1930s (McCown and Keith, 1939), there has been widespread recognition that there is a high level of anatomical variability in the southern Levantine Late Pleistocene (Vandermeersch, 1981, 1992; Hovers et al., 1995; Trinkaus, 1992, 1995; Wolpoff, 1999; Holliday, 2000). The current prevailing view is that some fossil specimens from the Levant (e.g., Tabun C1, Amud 1, Kebara 2; Dederiyeh) and the Zagros Mountains (multiple individuals from Shanidar Cave) show closest morphological affinity to European Neandertals (see below) and are referred to the species *Homo neanderthalensis* (or at least are recognized as members of the same lineage as the European Neandertals) by most paleoanthropologists (e.g., Vandermeersch, 1981, 1992, 1996; Trinkaus, 1983, 1992, 1995; Rak, 1990, 1998; Hovers et al., 1995; Holliday, 2000; Niewoehner, 2001). In contrast, some Late Pleistocene specimens from the southern Levant (specifically those from the sites of Skhul and Qafzeh) show greater affinity with *H. sapiens* than with Neandertals. Despite the fact that some have focused on the retention of archaic plesiomorphies in some Skhul-Qafzeh individuals (Corruccini, 1992; Kidder et al., 1992; Wolpoff, 1999), they are referred to *H. sapiens* by most paleoanthropologists (e.g., Vandermeersch, 1981, 1992, 1996; Tillier, 1999; Trinkaus, 1983, 1992, 1995, 2005; Rak, 1990; Hovers et al., 1995; Holliday, 2000), and in the vernacular are called "modern" or "nearly modern" humans.

While their preliminary report on the Mount Carmel skeletons agreed with the two-population (species?) view stated above (Keith and McCown, 1937), by 1939, McCown and Keith had interpreted the high degree of morphological variation at the Mount Carmel caves (at least as reflected in hominins from Tabun and Skhul) as being indicative of a single, highly variable Late Pleistocene population in the "throes of evolution," a view echoed more recently by Arensburg and Belfer-Cohen (1998) and Wolpoff (1999). This view may retain

some appeal in light of the recent evidence for interbreeding between *H. sapiens* and *H. neanderthalensis*—interbreeding that according to geneticists occurred in Western Asia. Nonetheless, due to differences in cranial and postcranial characters manifest between these two samples (see below), and as discussed above, most paleoanthropologists today hold the view that there are two distinct fossil hominin populations (or paleospecies) in the Late Pleistocene Levant, one referred to *Homo neanderthalensis*, and the second referred to *H. sapiens*.

In the 1984 Smith and Spencer volume, Trinkaus reviewed the paleontological evidence for hominin occupation of Western Asia (as evidenced in the southern Levant and Zagros Mountains) during the Late Pleistocene (Trinkaus, 1984). His view, which was representative of the prevailing opinions of the day, was that the Levantine and Zagros Mountain Neandertals antedated, and were likely ancestral to, the more modern-looking hominins from the southern Levantine sites of Skhul and Qafzeh, whom he believed to date to ca. 40 ka. However, beginning in 1987, thermoluminescence (TL) and electron spin resonance (ESR) dates indicated that while the then-recently discovered Kebara 2 Neandertal skeleton dated to ca. 60 ka (as expected), the hominin-bearing layers at the nearby site of Qafzeh, whose remains were deemed to be those of modern or nearly modern humans, were dated to ca. 90 ka, much earlier than anyone expected (Valladas et al., 1987, 1988; Grün and Stringer, 1991). Subsequent radiometric dates (McDermott et al., 1993) have confirmed the early dates for the modern-looking specimens from Qafzeh and Skhul (ca. 80–120 ka), while the Neandertals from Kebara and Amud are considerably later in time (ca. 50–60 ka). The dating (and even taxonomic affinities) of the Tabun C1 skeleton and C2 mandible remain somewhat enigmatic (Vandermeersch, 1981; Trinkaus, 1983, 1984; Grün and Stringer, 1991; Lieberman and Shea, 1994; Arensburg and Belfer-Cohen, 1998; Quam and Smith, 1998; Rak, 1998; Schwarcz et al., 1988; Stefan and Trinkaus, 1998; Millard and Pike, 1999; and see below), although Tabun C1 may date to as early as 170–180 ka (Mercier et al., 1995). If this early date for Tabun C1 (and its taxonomic status as a Neandertal) is accepted, then there may be a considerable period of temporal overlap between *H. neanderthalensis* and *H. sapiens* in the Levant, one longer than their apparent temporal overlap (or lack thereof) in Europe (Hublin et al., 1995; Trinkaus, 2006; Roebroeks, 2008; Golovanova et al., 2010). Indeed, the authors of the recent study that revealed genetic evidence for hybridization between Neandertals and modern humans argue that the introgression (i.e., genetic exchange via hybridization) between these two forms of hominin occurred not in Europe but in Western Asia (Green et al., 2010).

However, while an early date for Tabun layer C does not rule out some degree of temporal overlap between these two species of hominin, there are some problems with the notion of Neandertals and modern humans living “side by side” for long periods in Western Asia. First, if Tabun C1 does date to ca. 170–180 ka, (early MIS 6), it could represent an earlier (but ephemeral) intrusion of Neandertals into Western Asia during glacial time periods (Vandermeersch, 1992; Hublin, 1998). Second, if interbreeding were widespread and long-term between the two forms in Western Asia, then we should not expect the two groups to maintain their morphological distinctness; yet they do so both cranially and postcranially (Trinkaus, 1995, 2005; Rak, 1993, 1998; Holliday, 2000; and see below). The fact that these forms are distinctive suggests that contacts between the two in Western Asia were somewhat limited—an idea that is supported by paleoclimatic and faunal data. These data seem to indicate the two hominin species were in the Levant at different times and under different climatic regimes, with the modern humans expanding into the region from Africa during the warm MIS phase 5 and Neandertals dispersing into the region following the reglaciation of Europe associated with the onset of MIS Stage 4 at ca. 75 ka (Vandermeersch, 1981; Bar-Yosef, 1988; Condemi, 1991; Rak, 1993; Hublin, 1998; Shea, 2001; and see below). In this

light, if ecological change and/or Neandertal intrusion into the Levant caused, or was accompanied by, a modern human retreat back into Africa, or reduced *H. sapiens*' numbers (in terms of the archaeological record, there is no evidence for cultural superiority of the early modern humans of Skhul and Qafzeh over that of the Levantine Neandertals [Shea, 2001, 2007, 2008]), then the opportunities for long-term cultural/genetic exchange between the two populations are reduced.

Middle Pleistocene *Homo* in Western Asia

While there have been multiple recent discoveries from Late Pleistocene contexts in Western Asia since the 1990s (see below), and while a wealth of Early Pleistocene *Homo* skeletal data has since been recovered from the Georgian site of Dmanisi (Gabounia et al., 2002; Lordkipanidze et al., 2007), the Middle Pleistocene of Western Asia remains relatively poorly represented in the hominin fossil record. Three femoral shafts from Middle Pleistocene context are known (from Gesher Benot Ya'acov and Tabun E in Israel), and an isolated molar was also recovered from layer E at Tabun (Trinkaus, 1995). The longest- and best-known Middle Pleistocene fossil specimen from the region, however, is the anterior neurocranial and partial facial skeleton from the Galilean site of Mughareh-el-Zuttiyeh, unearthed in 1925, and dating to between 500 and 200 ka (Condemi, 1999; Freidline et al., 2012). More recently, deciduous and adult teeth from Qesem Cave in central Israel have been recovered from Middle Pleistocene (ca. 400–200 ka) contexts, associated with the Acheulo-Yabrudian industry (Hershkovitz et al., 2011). While some researchers have linked the Zuttiyeh (references in Sohn and Wolpoff, 1993) and Qesem (Hershkovitz et al., 2011) remains with later modern, or nearly modern, humans, the features that they share with modern humans are either plesiomorphic or show a high level of variation across *Homo*, and thus links between these Middle Pleistocene Levantine hominins with later hominins of any species are tenuous at best.

West-Central Asia

Central Asia is a largely steppic region, most of which falls under the rain shadow of one or more of the long east-west chains of southern Asian mountains associated with the uplift due to the merging of Asia proper with the Indian subcontinent. For this reason, it is a relatively dry environment that even today remains sparsely populated and that was likely cold and inhospitable for much of the Pleistocene. A Neandertal presence in Central Asia has been documented since the recovery of the juvenile skeleton from Teshik-Tash in Uzbekistan in 1938 (Okladnikov, 1939), although this specimen's Neandertal affinities, along with more recently discovered fragmentary remains from Obi-Rakhmat (Glantz et al. 2008), have been questioned by some (see below). There are not many other Late Pleistocene specimens yet recovered from this vast region. Trinkaus et al. (2000) described a deciduous mandibular second incisor found in Middle Paleolithic levels at the site of Khudji in Tajikistan. More recently, Late Pleistocene skeletal material has been recovered in and near the Altai Mountains of southern Siberia at the sites of Okladnikov and Denisova Caves (Krause et al., 2007, 2010; Reich et al., 2010), which, while skeletally undiagnostic in terms of taxonomy, have yielded radically different results with regard to their mtDNA affinities (see below).

The oldest known fossil hominin from the region, Teshik-Tash 1, has broadly been considered to be a Neandertal (Coon, 1962; Trinkaus and Howells, 1979; Stringer and Gamble, 1993; Rak et al., 1994; Franciscus, 1999; Schwartz and Tattersall, 2003; Bruner and Manzi, 2008; Wood and Lonergan, 2008; Cartmill and Smith, 2009), although there have been some

who since its discovery have continued to question its Neandertal affinities (Weidenreich, 1945; Wolpoff et al., 2004; Glantz et al., 2009). However, in 2007, it was revealed that the specimen had mtDNA sequences identical to those of other, undisputed Neandertal specimens (Krause et al., 2007). Among those for whom Teshik-Tash represented *Homo neanderthalensis*, the specimen was long considered the easternmost representative of that species (Trinkaus and Howells, 1979; Stringer and Gamble, 1993; Herrera et al., 2009), but mtDNA recovered from a 30–38 ka subadult humerus from the site of Okladnikov Cave in southern Siberia, some 2,000 km to the northeast of Teshik-Tash, also presented Neandertal sequences, which appear to indicate that Neandertals ranged even farther east than was previously accepted (Krause et al., 2007). Importantly, the fact that Krause et al. (2007) found no deep mtDNA divergence between European Neandertals and the Teshik-Tash and Okladnikov specimens lends credence to the hypothesis (discussed above) in which *Homo neanderthalensis* was a European species that only relatively recently immigrated into Western Asia.

In contrast, mtDNA recovered from an unpublished and undescribed distal fifth manual phalanx recovered only about 60 km away from Okladnikov Cave, in deposits dating to ca. 48–30 ka, at Denisova Cave in the Altai Mountains, presented mtDNA sequences never before observed among recent or fossil hominins (Krause et al., 2010). An mtDNA phylogeny of one Pleistocene modern human and fifty-four recent humans, six Neandertals, and the Denisova hominin, constructed using a Bayesian approach, indicated a deep mtDNA divergence between Denisova and all other hominins, with an estimated lineage divergence time of approximately 1.0 million years (Krause et al., 2010). In contrast, when nuclear DNA was extracted from the Denisova phalanx, and a neighbor-joining tree was constructed using these data, it still indicated a divergence between Denisova and the Neandertals but reduced the estimated time depth of that divergence and made the Denisova hominin an outgroup to the Neandertals, who show little divergence from each other (Reich et al., 2010). Importantly, too, Denisova nuclear DNA sequences are retained in a recent human Melanesian sample, indicating that this (as yet) taxonomically unassigned hominin contributed genes to at least some modern humans.

Both Krause et al. (2010) and Reich et al. (2010) interpret the above results as indicating the presence of a heretofore unknown hominin in Late Pleistocene Central Asia (but see Trinkaus, 2010). The Late Pleistocene date of the Denisova specimens and their proximity to Okladnikov Cave make it surprising that both the mtDNA and nuclear DNA signatures are so different from those of Neandertals, given that according to all genetic analyses done to date Neandertals (like modern humans, and unlike African apes or orangutans) appear to have been characterized by relatively low levels of intrapopulational genetic variability (Gagneux et al., 1999; Krings et al., 2000; Kaessmann et al., 2001; Schmitz et al., 2002; Serre et al., 2004; Caramelli et al., 2006; Krause et al., 2010). One intriguing possibility is that West-Central Asia represents both the easternmost fringe of the *Homo neanderthalensis* range and the westernmost margin of the *Homo erectus* range, with these two paleospecies coming into sporadic contact with each other in the Late Pleistocene.¹

Body Size and Shape

European Neandertals have long been known for their stocky bodies, short stature, and reduced distal limb lengths (Coon, 1962; Badoux, 1965; Trinkaus, 1981; Churchill, 1996, 1998; Holliday, 1997a). These features have most frequently been related to selection due to the glacial cold that so frequently characterized Europe during the Pleistocene (Badoux, 1965; Trinkaus, 1981; Holliday, 1997a; Steegmann et al., 2002). The specific mechanism theorized to be responsible for these proportions is that a wider, larger trunk and shorter limbs

give the bodies in which they are found relatively less surface area (i.e., a lower surface area to volume ratio), and since heat is lost through the body's surface, these shape differences enhance the body's ability to retain heat in cold conditions. Given that the climate of the Levant was less impacted by Pleistocene global cooling, even during glacial maxima (CLIMAP, 1976, 1981; Mellars, 1996), it is expected that Western Asian Neandertals would be characterized by less cold-adapted body shape and limb proportions. This does in fact appear to be the case. Unlike European Neandertals, Western Asian Neandertals are not characterized by low brachial (radius length:humerus length) indices, which tend to be associated with cold climates among recent humans (Trinkaus, 1981; Franciscus, 1989; Holliday, 1995). However, crural (tibia length:femur length) indices are low in both European and West Asian Neandertals (Trinkaus, 1981; Franciscus, 1989; Holliday, 1995). European Neandertals have also been demonstrated to have limb:trunk proportions not unlike those found in modern-day circumpolar groups (Holliday, 1997a). While preservation problems prevent limb:trunk proportions from being assessed in West Asian Neandertals (except for the upper limb of the Kebara 2 specimen), limb length and articular size data can be assessed in a multivariate sense to gauge these hominins' total morphological pattern with regard to size and shape. Multivariate cluster analyses of such postcranial data tend to cluster European Neandertals with modern-day circumpolar groups (Holliday, 1997a). In contrast, similar multivariate assessments of body shape (principal components analysis and discriminant analysis of log shape data) indicate that West Asian Neandertals are significantly less cold-adapted; they show a closer affinity in body shape to modern-day Europeans (Holliday, 2000).

With regard to stature among the Late Pleistocene West Asian hominins, Trinkaus (1995) suggests there is a hint that Western Asian Neandertals, with (probable) females exhibiting statures from ca. 150 to 160 cm, and (presumed) males exhibiting statures from ca. 165 to 185 cm, were slightly taller than their European conspecifics, but their ranges of variation overlap considerably, and the differences between the European and Western Asian means are statistically insignificant. In contrast, according to Trinkaus (1995) the Skhul-Qafzeh samples are much taller, with female stature averaging ca. 170 cm and males averaging ca. 185 cm, which is taller than the Endo and Kimura (1970) stature prediction for the tallest Western Asian Neandertal, Amud I. Stature in humans is developmentally labile (Tanner et al., 1982; Steckel, 1987; Eveleth and Tanner, 1990; Takamura et al., 1988; Jantz and Jantz, 1999; Bogin et al., 2002) and often reflects the nutritional and/or health status of the populations in question. In contrast, while there is developmental plasticity in limb proportions (Weaver and Ingram, 1969; Serrat et al., 2009), proportions tend to be relatively stable across multiple millennia in migrants or presumed migrant populations (Holliday, 1995; 1997b). In this regard, it is of interest that the Skhul-Qafzeh samples are characterized by a more tropically adapted body shape than the Western Asian Neandertals. For example, Skhul 4 (and almost certainly Qafzeh 9, although this specimen's pelvis shows great postmortem distortion) had relatively narrow bi-iliac (pelvic) breadths, while the Kebara 2 and Tabun C1 Neandertals are characterized by wide bi-iliac breadths (Rak, 1990; Weaver and Hublin, 2009). The Skhul-Qafzeh samples are also characterized by higher crural indices than are the Western Asian Neandertals (Trinkaus, 1981, 1995), although the two samples have similar brachial indices (Trinkaus, 1981, 1995; Franciscus, 1989). Multivariate analyses of body shape indicate that with the exception of Skhul 5, the Skhul-Qafzeh samples have closest affinity in body shape to recent sub-Saharan Africans, while as mentioned above, the majority of the West Asian Neandertals are more similar to recent Europeans (Holliday, 2000).

This pattern is perhaps best interpreted as indicating that the Skhul-Qafzeh samples are descended from early modern humans that evolved first in East Africa ca. 200 ka and are

represented by Ethiopian specimens such as Omo-Kibish I at ca. 195 ka and Herto at ca. 160 ka (Day and Stringer, 1982; White et al., 2003; Clark et al., 2003; McDougall et al., 2005). These modern, or nearly modern, humans expanded into North Africa and the Levant perhaps as early as 124 ka, likely taking part in the warm-climate mammalian expansion associated with the warming trend of MIS 5e (the last Interglacial). This scenario finds support in the faunal record from Qafzeh. According to Tchernov (Rabinovich and Tchernov, 1995; Tchernov, 1998) the fauna at Qafzeh are said to include a strong Afro-Arabian element. For example, two genera of mice that today are endemic to Africa (*Praomys* and *Arvicanthis*) are found in Qafzeh Mousterian levels (Tchernov, 1988, 1998).

In contrast, the fact that the West Asian Neandertals retain at least some “cold-adapted” features found in circumpolar people today (e.g., low crural indices, wide pelves) is consistent with the view that they represent relatively recent immigrants into Western Asia from Europe. Faunal data seem to corroborate this view. If, for example, Tabun layer C dates from the late MIS 5 and well into early MIS 4, then there appears to be faunal evidence there for a shift from a more Afro-Arabian faunal spectrum to a more Euro-Siberian one (Tchernov, 1988, 1998). Many of the warm-adapted mammalian species, including the two (African) genera of mice mentioned above, disappear from the southern Levant, and many cold-adapted taxa not found at Qafzeh mark their first appearance in the Levant (Tchernov, 1992). If Tabun layer C was deposited by Neandertals, then it seems likely that they too were among the new cold climate fauna. This presumed expansion of Neandertals into the Levant (which may be better characterized as a retreat from colder areas to the north) is associated with the drop in global temperatures that occurred at the beginning of MIS 4 (ca. 75 ka). These Neandertal immigrants may have then displaced their warm climate cousins, as there is no solid evidence for technological superiority by either paleospecies. However, it seems equally probable that the shift in global climate stimulated a retreat of the population represented by the Skhul-Qafzeh hominins back into Africa prior to any long-term contact with the “invading” Neandertals. However, as discussed in detail below, if Tabun C1 is both a Neandertal and early, it substantially complicates this picture.

Recent analyses of Levantine Neandertal thoracic morphology in comparison to European Neandertals, Skhul-Qafzeh, early Upper Paleolithic, and extant comparative samples further adds to this picture. Neandertals clearly possessed a comparatively capacious thorax (Franciscus and Churchill, 2002; Sawyer and Maley, 2005; Weinstein, 2008; Gómez-Olivencia et al., 2009). Moreover, based on the exceptionally complete thorax of the Levantine Kebara 2 individual, it is the midthoracic region that is particularly large in Neandertals, producing a somewhat “hyper-barrelshaped” configuration (Gómez-Olivencia et al., 2009). There also appear to be few, if any, indicators for ecogeographical differences between European and Levantine thoracic anatomy as was previously suggested, particularly with respect to upper thoracic dimensions (Churchill 1994a,b; Franciscus and Churchill, 2002), although this question remains open (Gómez-Olivencia et al., 2012). Both European and Near Eastern Neandertals also have comparatively larger and more rounded rib shaft cross-sectional areas (i.e., greater robusticity) across individual rib shafts in both the midthoracic and lower thoracic ribs (Franciscus and Churchill, 2002). In contrast, the early modern Skhul-Qafzeh sample is much more similar to extant humans in this regard with flatter rib shafts, particularly in the upper portion of the thorax. These analyses contradict the view of Arensburg (1991), whose comparative analysis of the Kebara 2 Neandertal ribs with modern humans, including observations regarding the Skhul-Qafzeh rib remains, indicated essentially no anatomical differences, and in most cases the more recent results support the much earlier analysis of McCown and Keith (1939), who saw striking differences between the thoracic anatomy of the Tabun C1 Neandertal and the anatomically modern Skhul remains.

While clinical studies indicate that the relationship between a large skeletal rib cage and a large pulmonary capacity is not isomorphic (e.g., Bellemare et al., 2001), studies of modern human high-altitude-adapted populations show both higher vital capacities and chest circumferences compared to lowland populations (Hurtado, 1932; Weinstein, 2007). In this regard, the larger chest of Neandertals compared to modern human groups has been linked to differences in daily energy and oxygen consumption. While estimates of TEE (total energy expenditure) for Neandertals vary, all are larger than those of modern human groups (Sorensen and Leonard, 2001; Steegman et al., 2002). A comparison of the raw variables for stature and body mass used by Churchill (2006) to calculate TEE indicates that Middle Pleistocene individuals would have estimated values equal to or greater than those estimated for Neandertals. If true, Neandertals would likely have inherited relatively large chests from their Middle Pleistocene ancestors (Franciscus and Churchill, 2002; Gómez-Olivencia, 2009) that would have been advantageous in cold climate environments due to a higher heat production tied to high caloric intake (Churchill, 2006). However, it is important to be clear that this would have been the result of an *exaptation*, rather than cold-adaptation per se. Moreover, a large chest would be necessary for the increased oxygen consumption derived from higher energetic demands of a larger body mass compared to modern humans, regardless of their subsistence economy (Gómez-Olivencia, 2009), which likely explains the striking differences in chest morphology between Neandertals and the early modern humans from Skhul-Qafzeh despite a common Middle Paleolithic techno-cultural base.

Locomotion

It has long been recognized that robusticity of the postcranial skeleton, for which “robusticity” is defined as “the strength or rigidity of a structure relative to the mechanically relevant measure of body size” (Ruff et al., 1993: 25), shows a general downward trajectory within the genus *Homo* from the Early Pleistocene to the Holocene (Ruff et al., 1993). Therefore it is not surprising that the Late Pleistocene inhabitants of Western Asia, whether the Skhul-Qafzeh or Neandertal populations, tend to be characterized by more robust lower limbs than those of modern-day inhabitants of the region.

Variability in postcranial robusticity, in particular differences in long bone diaphyseal mechanical properties, is generally interpreted as phenotypically plastic features that reflect response(s) to the mechanical forces that act upon them during the life of the individual (Lanyon, 1982; Cowin, 1989). While there is evidence for (genetic and/or ontogenetic) integration of the hominin postcranium, it has also been demonstrated that there is a high tolerance in the postcranial skeleton for such phenotypic plasticity in response to biomechanical forces (Churchill, 1996). Therefore, differences in postcranial robusticity, especially diaphyseal robusticity of the humerus, femur, and tibia, have played an important role in interpretation of potential behavioral differences between the Skhul-Qafzeh hominins and the Levantine Neandertals.

With regard to the lower limb, Trinkaus (1983) argued that the West Asian Neandertals evinced extremely robust tibial shafts, while the Skhul-Qafzeh hominins showed more modest robusticity of that bone (albeit higher than that of Holocene humans). Similarly, the Skhul-Qafzeh sample was found to exhibit higher neck-shaft angles and lower midshaft robusticity than the West Asian Neandertals (Trinkaus, 1986, 1992, 1993a). These data were interpreted as indicative of a significant difference in the types of biomechanical loads experienced by the lower limb skeleton in these two samples, with the Neandertals experiencing either higher peak loads or (more likely) experiencing longer duration(s) of lower limb biomechanical loads (Trinkaus, 1983, 1986, 1992). Similarly, Rak (1990) explored differences in

pelvic morphology between Qafzeh 9 and the Kebara 2 Neandertal and argued that there were key shape differences between the two hominins that likely reflected locomotor differences between the taxa from which they were drawn. These lines of research lead to interesting cross-fertilization of ideas between biological anthropology and archaeology, becoming incorporated into hypotheses that the Neandertal adaptive strategy was more predatory/carnivorous than that of the Skhul-Qafzeh hominins (Shea, 1998), or that in the southern Levant the Neandertals followed a “radiating” (what Binford [1980] would refer to as “collecting”) strategy, while the Skhul-Qafzeh hominins followed a “circulating” (what Binford [1980] would refer to as “foraging”) strategy (Lieberman and Shea, 1994). However, despite the appeal of these cross-disciplinary hypotheses, by the late 1990s they had fallen into disfavor. Work by Trinkaus and colleagues found that once scaled to “biomechanically appropriate measures of body mass and beam length” (Trinkaus and Ruff, 1999a:1289), the differences in femoral and tibial diaphyseal strength between Qafzeh-Skhul and the West Asian Neandertals disappeared (Trinkaus et al., 1998; Trinkaus and Ruff, 1999a,b). Likewise, Lieberman (1998) found no evidence for differences in cranial vault thickness between the two Levantine Late Pleistocene taxa, which he interpreted as indicating similar activity levels between the Skhul-Qafzeh and Neandertal samples. Based on these analyses, then, the lower limb diaphyseal strength data do not lend support to hypothesized differences in locomotor behavior between the two samples—rather, the slender appearance of the Skhul-Qafzeh long bones is more readily attributed to differences in body proportions and body mass due to their presumed relationship to the earliest modern humans from East Africa (Holliday, 1997b, 2002; Trinkaus and Ruff, 1999a,b; Pearson, 2000).

Birthing

Late Pleistocene Levantine individuals preserving significant portions of taphonomically fragile and therefore relatively rare pelvic elements of the birth canal have figured prominently in recent discussions of the evolution of modern birthing dynamics. Human birthing is difficult owing to a trade-off between large neonatal brain size and maternal pelvic dimensions, which are constrained by aspects of bipedal biomechanics resulting in a rotational pattern of birth through the tightly configured pelvic planes leading to a unique pattern of assisted birth (obligate midwifery) with important social dynamics (Rosenberg and Trevathan, 2002).

Obstetrical difficulties and some form of birthing assistance may have arisen at the outset of hominin evolution in concert with bipedalism (Rosenberg and Trevathan, 2001), yet it seems likely based on the few preserved Pliocene female pelves that birth in australopiths was non-rotational, with the long axis of the neonate’s head oriented transversely as it moved through the three birth canal planes (Tague and Lovejoy, 1986). The extant human pattern of rotational birth, along with intensified and obligate midwifery, most likely emerged later when a critical threshold of brain size attainment in *Homo* was added to the shared hominoid pattern of broad, rigid shoulders (Trevathan and Rosenberg, 2000).

Until recently, the consensus has been that rotational birth was not present in Early Pleistocene *Homo* (Ruff, 1995), confirmed by the discovery of a largely complete 1.4–0.9 ma female *Homo erectus* pelvis from Gona, Ethiopia (Simpson et al., 2008), with the primitive non-rotational pattern persisting until the Middle Pleistocene (Ruff, 1995). Resolving the appearance of rotational birth more precisely has been hindered by the paucity of fossil pelvic remains, especially from females, due to the fragility of pelvic bones. Over the past 25 years, rotational birth has been inferred for archaic *Homo sapiens* based largely on three specimens: Sima 1, a 600 ka male pelvis from the Sima de los Huesos, Spain (Arsuaga et al.,

1999b; Bischoff JL et al., 2007), a 260 ka left os coxae belonging to a partial female skeleton from Jinniushan, China (Rosenberg, 1998; Rosenberg et al., 2006; see also chapter 3 this volume), and a 60ka partial pelvis from the male Levantine Neandertal, Kebara 2 (Rak, 1991). Nonetheless, it has always been recognized that extrapolating female birth canal shape from male pelvic remains is uncertain. Moreover, while the inlet anatomy of the female Jinniushan specimen can be estimated (Rosenberg et al., 2006), the midplane and outlet dimensions are unknown.

In light of this, Weaver and Hublin (2009) recently refocused efforts on the Levantine Tabun C1 female Neandertal pelvis (McCown and Keith, 1939), which retains portions of the left pubis and ilium, as well as the right pubis, ischium, and ilium, using computerized virtual reconstruction. The Weaver and Hublin reconstruction was actually the second modern-day effort. In a study assessing Neandertal neonatal brain size and subsequent brain growth relative to recent modern humans to compare life history rates, a virtual reconstruction of the Tabun C1 pelvis was conducted by Ponce de Léon et al. (2008), which was used to simulate the birth process in Neandertals using a complete neonatal skeleton from Mezmaiskaya Cave, Russia (Golovanova et al., 1999). In their reconstruction of the Tabun C1 pelvis, Ponce de Léon and colleagues argued that the midplane and outlet configuration could not be established from the fossil elements alone due to an inability to accurately infer the ischial and sacral orientations. Consequently, they assumed the modern human rotational pattern for the Mezmaiskaya neonate and modern human cephalopelvic proportions in order to parameterize the reconstructed birth dimensions.

Weaver and Hublin (2009) focused on parturition itself, asking whether Neandertal females, represented by the Tabun C1 pelvis, actually had the same birth canal size and shape proportions as recent humans, and thus rotational birth, which was assumed in the Ponce de Léon et al. study. The resulting birth inlet and outlet areas of Tabun C1's reconstructed pelvis were very similar to the mean area value for a geographically diverse sample of recent modern female pelves; however, birth canal *shape* in Tabun C1 in terms of the inlet index (anteroposterior breadth/transverse breadth) at 0.79 was low compared to recent human females, and her outlet index at 0.70 was found to be extremely low, in fact, falling entirely out of the range of Weaver and Hublin's global comparative sample. Compared to the characteristically anteroposteriorly oval outlet in modern humans, Tabun C1's birth outlet in their reconstruction is transversely oval. While poor preservation of the ischial spine precludes definitive assessment of the midplane, the results for the outlet shape in Tabun C1 from this study indicated that Neandertals had a different birthing pattern from modern humans. Rather than rotating so that the head is anteroposteriorly oriented (facing away from the mother at birth), Neandertal neonates would have aligned their heads transversely exiting through the birth outlet.

If accurate, these divergent Neandertal and extant modern human birthing patterns bear on several issues. Despite its male attribution, Sima 1 best represents pelvic shape in the last common ancestor of Neandertals and humans (Arsuaga et al., 1999b), and it clearly possesses a transversely oval outlet. Weaver and Hublin argue that Middle Pleistocene encephalization trends (Bruner et al., 2003) increased obstetric constraints in both the Neandertal and modern human lineages with divergent results. Neandertals continued to expand transverse pelvic outlet dimensions (the primitive condition), commensurate with large bi-iliac breadths and cold-adaptation, with secondary consequences such as more or less equal pubic bone lengths in both Neandertal sexes (Rosenberg, 1998). Modern humans, in contrast, underwent anteroposterior expansion of the birth outlet since African origins for modern humans were built on a transversely narrow pelvis bauplan related to warmer climate that had been argued to be present in the 1.53 ma juvenile male skeleton (KNM-WT 15000) from Kenya (Ruff and Walker, 1993). The earliest evidence for this anatomy in early

modern humans is evident in the ca. 100 ka Levantine early modern Skhül 4 pelvis, and even though distorted, is also apparent in the coeval Levantine Qafzeh 9 pelvic remains (see above). The new wide-hipped female *Homo erectus* pelvis from Gona (Simpson et al., 2008) complicates this climatic explanation and provides evidence for continuity in wide bi-iliac breadths from *Australopithecus* to Neandertals. New interpretations of the thorax in Neandertals (Gómez-Olivencia, 2009; see above) mirror this by postulating that a wide body with high body mass represents the primitive hominin condition retained in Neandertals, which, if related to cold adaptation in Neandertals, represented an exaptation rather than cold adaptation per se.

While the female Tabun C1 pelvic remains are likely to be more relevant to birthing patterns than are male pelves, even well-preserved ones, it remains uncertain whether key potential sources of reconstruction error in Tabun C1 (i.e., the estimation of the sacral landmarks, and the orientation of the pubis fragment relative to the hip joint and other elements of the hemipelvis) can be overcome even with virtual reconstruction techniques. It should also be noted that any differences in the precise birthing pattern between Neandertals and modern humans that might have existed are unlikely to alter the fact that both lineages would have most likely had difficult births, obligate midwifery, and all of the attendant social implications (Franciscus, 2009).

Manipulation

Fossil hominin habitual manipulative repertoires are primarily reflected in the bones of the hand and arm. Trinkaus (1995) argues that some information regarding these habitual behaviors is also evident in the thoracic skeleton (due to the importance of the thoraco-scapular and thoraco-humeral muscles in use of the upper limb) and in the anterior dentition when paramasticatory use of the teeth is evident (which also has skeletal correlates in the upper axial skeleton).

In the upper limb skeleton proximal to the hand and wrist, Western Asian Neandertals are characterized by muscular hypertrophy as reflected in the breadth of the scapula, size of the *M. pectoralis major* insertion, and the bowing of the radius (Trinkaus, 1995). Trinkaus and colleagues' work also indicates that many Neandertal upper limb muscles operated with greater mechanical advantage than those of the Skhül-Qafzeh sample, as reflected in longer clavicles and the more medial rather than anteromedial orientation of the radial tuberosity (Trinkaus and Churchill, 1988; Trinkaus, 1995). Likewise, the more robust and markedly more horizontally oriented cervical spinous processes of the West Asian Neandertals (Stewart, 1962; Trinkaus, 1983; Arensburg, 1991) have been linked to the idea of more frequent reliance on the use of their teeth as tools. The idea of increased reliance on paramasticatory behavior (see next section) has also been argued to be reflected in the anterior tooth wear patterns of the two groups, for which the West Asian Neandertals show greater anterior wear than do the Skhül-Qafzeh hominins (Trinkaus, 1992).

With regard to the hand and wrist, West Asian Neandertal hand skeletons also show greater muscular hypertrophy than those of the Skhül-Qafzeh sample, as reflected in the presence of large crests for *M. opponens pollicis* and *M. opponens digiti minimi* on MC 1 and MC 5, respectively, and more prominent ridges for the insertion of the flexor tendon sheaths on their proximal phalanges (Trinkaus, 1983, 1995; Maki and Trinkaus, 2011; Niewoehner, 2006). Compared to Neandertals, the Skhül-Qafzeh sample exhibits reduced mechanical advantages throughout the wrist and hand due to the decreased relative projection of their trapezium, hamate, and scaphoid tubercles and their thumb phalanx length proportions (Niewoehner, 2006). Trinkaus and Villemeur (1991) note that Neandertals, compared to

extant human populations, have increased mechanical advantages in their thumb metacarpophalangeal joints due to their significantly higher distal to proximal phalangeal length ratios combined with their dorsopalmarly tall proximal phalanx base articular heights. In contrast, the Qafzeh 9 metacarpophalangeal joint mechanical advantage and phalangeal length ratio do not differ significantly from the average values for European Upper Paleolithic and extant human samples (Niewoehner, 2006). One exception to this pattern is reported by Maki and Trinkaus (2011), who argue that both the Neandertals and the Skhül-Qafzeh hominins had similar levels of mechanical effectiveness of their *opponens pollicis* muscles. Additional evidence for the inferred grip strength of the Neandertal hand is provided by the morphology of their distal phalangeal tuberosities, which were moderately radioulnarly expanded and dorsopalmarly thick relative to extant human samples. The Neandertal morphology is indicative of wider fingertips, the larger tuberosities providing increased attachment area for the pulp and the nail, and is most likely an adaptation for effectively transmitting large loads across the fingertips (Trinkaus, 1983). The radioulnar breadth and dorsopalmar thickness of the Qafzeh 7 and Qafzeh 9 distal tuberosities, however, are well within the combined European Upper Paleolithic and extant human range of variation (Trinkaus, 1983; Niewoehner, 2006).

West Asian Neandertal carpometacarpal articulations are characterized by joint shapes and orientations that differ significantly from those of the Skhül-Qafzeh hominins, as well as those of European Upper Paleolithic and extant human samples (Trinkaus and Villemeur, 1991; Niewoehner et al., 1997; Niewoehner, 2001, 2006). Based on the morphology of the Neandertal capitate-to-MC2/3 articulations, it appears that the major reaction forces moving through their hands were non-oblique, suggesting that their behavioral repertoire did not include habitual use of hafted tools requiring the use of oblique power grips (Niewoehner et al., 1997; Niewoehner, 2001; but see Maki and Trinkaus, 2011). Analysis of 3D coordinate data taken on carpal and proximal metacarpal facets (including the functionally important MC 1 and MC 3 bases and trapezia) indicates that the Skhül-Qafzeh carpometacarpal articulations are morphologically and functionally more similar to those of European Upper Paleolithic samples, rather than those of the West Asian Neandertals (Niewoehner, 2001).

In sum, West Asian Neandertal hands are adapted primarily to produce increased grip strength during circumduction of the thumb at the trapezio-metacarpal 1 joint, during cupping of the palm through the opposition of the fifth metacarpal, during flexion of the wrist and adduction of the hand, and during flexion of the thumb metacarpophalangeal joint. The Neandertal functional complex aided in the production of a powerful vice-like precision grip for the use of unhafted flakes, as well as for the use of primarily transverse, rather than oblique, power grips. Alternately, the Skhül-Qafzeh hand remains (though not precisely the same in morphology and functional anatomy) most closely resemble the hand remains of European Upper Paleolithic humans whose hands are functionally suited for finer, more precise finger movements, as well as for the preferential use of oblique power grips necessitated, perhaps, by the use of hafted tools (Niewoehner, 2001, 2006). Among the Skhül-Qafzeh sample, the use of (hafted?) tools, giving them more of a mechanical advantage than those used by the West Asian Neandertals, is likely also reflected in the diaphyseal robusticity of their humeri (Trinkaus and Churchill, 1999). Specifically, while having similar diaphyseal cross-sectional shapes, the West Asian Neandertals have more robust humeral shafts as reflected in both cortical area and polar moments of area relative to humeral length (Trinkaus and Churchill, 1999). In light of the paleobiological evidence, then, it is somewhat surprising that there is little evidence of a technological difference between the lithic components of the Mousterian toolkits used by these two groups (Shea, 2001, 2008).

Craniofacial Form

Craniofacial form has long been emphasized in hominin taxonomic and phylogenetic studies in general, and it has played an important role in deciphering the patterns of Late Pleistocene human evolution in Western Asia. The taxonomic affinities of the fragmentary fronto-facial remains of Zuttiyeh (Galilee, Israel; Figure 2.1) associated with Acheulo-Yabrudian artifacts and dated broadly to between 500 and 200 ka (Bar-Yosef, 1995; Condemi, 1999; Freidline et al., 2012) have been a matter of longstanding debate. Early work (Keith, 1927) considered it to have Neandertal affinities. More recent studies have suggested it as a lineal predecessor of the modern human Skhül-Qafzeh group (Vandermeersch, 1989, 1995), a generalized form of archaic *Homo* (Rak, 1986; Trinkaus, 1989; Simmons et al., 1991; Rightmire, 2009), or as showing affinities with Asian *H. erectus* (Sohn and Wolpoff, 1993). In arguably the most comprehensive analysis of the Zuttiyeh remains to date, Freidline et al. (2012) conclude that it is difficult to categorically ascribe it to any one taxonomic allocation but note that its mosaic morphological pattern is indicative of the population that gave rise to Neandertals and modern humans. The incompleteness of the Zuttiyeh remains is likely a factor in this taxonomic ambiguity given that the frontal bone, while containing features that are often heavily emphasized in Middle to Late Pleistocene hominin taxonomy, by itself may provide somewhat limited information (Athreya, 2006; Freidline et al., 2012).

The 120–90 ka Skhül-Qafzeh sample includes several fairly complete adult crania or major craniofacial elements including Skhül 4, 5, 9, and Qafzeh 6 and 9. The well-known Skhül 5 (Figure 2.2) and Qafzeh 9 (Figure 2.3) skulls have tended to be emphasized likely due to the fact that both retain well-preserved crania and associated mandibles, although the midfacial region of Skhül 5 is missing. The sample is characterized by neurocrania that exhibit several modern human features including high, vertical frontals, parietal expansion



Figure 2.1. Lateral view of the Zuttiyeh anterior craniofacial skeleton from Israel. From Cartmill and Smith (2009). Used with permission. © Matt Cartmill.

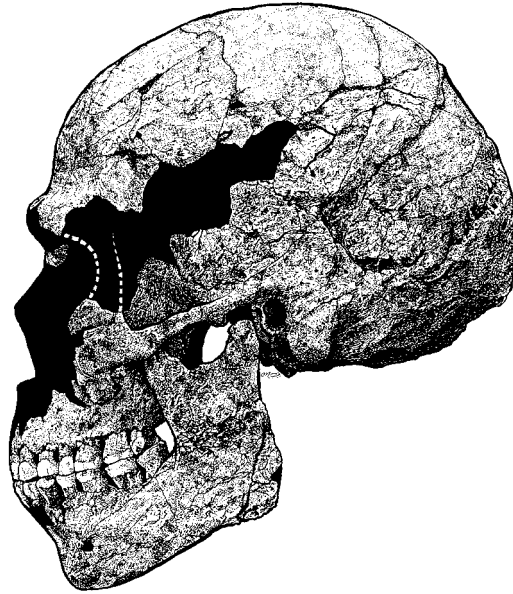


Figure 2.2. Lateral view of the Skhul 5 skull from Mt. Carmel, Israel. From Cartmill and Smith (2009). Used with permission. © Matt Cartmill.



Figure 2.3. Lateral view of the Qafzeh 9 skull from Israel. From Cartmill and Smith (2009). Used with permission. © Matt Cartmill.

resulting in a pentagonal configuration in occipital view, occipital rounding in lateral view, all of which collectively results in a globular neurocranium with a high rather than low overall cranial vault. Additional diagnostically modern human neurocranial features include the absence of a *true* suprainiac fossa (see Balzeau and Rougier, 2010), but with a distinct

external occipital protuberance, reduced or absent juxtamastoid eminences, and laterally pronounced/prominent mastoid processes.

The facial morphology of the Skhül-Qafzeh sample also exhibits key modern human features including reduced vertical facial dimensions and reduced facial prognathism, a midfacial infraorbital region usually possessing a canine fossa, relatively coronally oriented infraorbital surfaces, and a mandibular mental protuberance or tuber symphyseos projection, and anterior dental size reduction. Moreover, when accounting for the effects of developmental age, and when preserved, these craniofacial features also characterize the subadults in the Skhül-Qafzeh sample (Tillier, 1999, 2007).

Yet a high degree of variation within this essentially “modern” configuration has long been noted. Some craniofacial features of the Skhül-Qafzeh sample retain a more primitive configuration. For example, the supraorbital region is large compared to most extant human samples, and some individuals, such as Skhül 5, possess a supraorbital torus, which while thinner in its lateral components is continuous medially, forming a small supratrochlear sulcus. The supraorbital region in extant modern humans and early Upper Paleolithic samples characteristically lacks a torus, instead showing distinct medial (glabellar) midorbital and lateral arch components (although the glabellar components can still be quite large and projecting). However, not all of the Skhül-Qafzeh sample shows the primitive supraorbital configuration with Skhül 2, as well as Qafzeh 3, 6, and 9 showing the modern form instead. The latter individuals also possess smaller and more gracile faces compared to the markedly larger and more robust faces found in Skhül 4, 5, and 9. Some variation also exists in the topographical configuration of the infraorbital region; recent 3D geometric morphometric analysis shows that Skhül 4 displays a much flatter configuration than the inflected, canine fossa topography evident in Qafzeh 6 (Maddux and Franciscus, 2009; Maddux, 2011). Similarly, the mandibular remains of Skhül 4, 5, and 6 possess retromolar spaces (a trait that is evident in high frequencies among European and Western Asian Neandertals); however, a retromolar space is absent in Skhül 7 and Qafzeh 9 (Franciscus and Trinkaus, 1995). Variation in the precise configuration of the chin in the Skhül-Qafzeh sample has also been noted with only Qafzeh 8, 9, and 11 (the latter a subadult) possessing the inverted “T” mental trigone configuration with lateral tubercles and mental fossae thought to characterize modern humans (Schwartz and Tattersall, 2000, 2003), although these particular features are frequently absent even among individuals in extant comparative human samples (Bräuer, 2008).

Overall multivariate craniofacial analyses have, in some cases, produced results showing that the Skhül-Qafzeh sample cannot be differentiated from Levantine Neandertals (Simmons et al., 1991; Kramer et al., 2001; Wolpoff and Lee, 2001), and others have concluded that some of the Skhül-Qafzeh individuals are more archaic than post-50 ka modern humans (Corruccini, 1992; 1994; Kidder et al., 1992; Schillaci, 2008; see also Guatelli-Steinberg and Reid, 2010, for an example of this in terms of tooth morphology and development). Nonetheless, there is fairly broad consensus today based on other multivariate analyses combined with univariate, bivariate, and discrete analyses that the Skhül-Qafzeh sample collectively represents a robust but fundamentally modern human pattern of craniofacial anatomy that can be differentiated from the Levantine and other Western Asian Neandertals (e.g., Lieberman et al., 2002; Trinkaus, 2005, 2006; Tillier, 2007; Cartmill and Smith, 2009; Rightmire, 2009; Maddux and Franciscus, 2009; Harvati et al., 2010; Maddux, 2011).

The non-modern Middle Paleolithic sample in Western Asia is represented by chronologically earlier and later samples of adult and subadult Neandertals. The craniofacial anatomy of the later group (Shanidar 1 and 5; Amud 1 and 7; Dederiyeh 1 and 2), in general, shows strong similarities to that of the “classic” beginning MIS 4 Neandertals of Europe (Franciscus, 2002; Bailey, 2004; Trinkaus, 2006; Cartmill and Smith, 2009; see chapter 6,

this volume). These derived Neandertal neurocranial features include parietal curvature resulting in an oval or “en-bombe” configuration in occipital view, arguably *true* suprainiac fossae (Balzeau and Rougier, 2010), relatively small and downwardly positioned posterior inner ear semicircular canals, an elongated foramen magnum, and an enlarged or inflated juxtamastoid eminence that superficially makes the adjacent mastoid processes appear diminutive. Derived midfacial features include parasagittally aligned infraorbital surfaces² extending to an anterolaterally flattened zygomatic region, relatively broad anteroinferior nasal bones associated with an anterior eversion of the frontal processes of the maxillae (producing a square-shaped piriform aperture), and a prominent and complex inferior nasal sill. Key mandibular features include a laterally placed and inferiorly positioned mandibular condyle, large superior medial pterygoid tubercles, lingular bridging (horizontal-oval form) of the mandibular foramen, and a high frequency of retromolar spaces. Additionally, the most salient derived dental features are several likely co-occurring occlusal details of the lower second premolar, a high frequency of lower molar midtrigonid ridges, and several details relating to upper M1 cusp proportions.

While not all of these features are present or diagnosable in all Western Asian individuals (dependent on preservation), there is wide consensus that the chronologically later adults (Shanidar 1 and 5, Amud 1, Kebara 2) and the subadults (Amud 7 and Dederiyeh 1 and 2) conform to this classic Neandertal craniofacial pattern (Suzuki, 1970; Trinkaus, 1983; Rak et al., 1994; Dodo et al., 1998; Akazawa et al., 2002a). Nonetheless, on the basis of geographic dispersion alone, we would expect morphological variability between European and Western Asian Neandertals in light of the fact that the two regions are geophysically (and climatically) separated by the Mediterranean Sea, the Black Sea, and the foothills of the Caucasus Mountains. Moreover, as Vandermeersch and Garralda (2011) have emphasized, population variation *within* Western Asia is expected as well, given the wide range of site dispersal; the Amud and Shanidar sites, for example, are separated by ca. 1,000 km.

These geographical considerations are related to varying interpretations of the Central Asian Teshik-Tash cranium and mandible discovered in 1938 in southeastern Uzbekistan and the eastern extent of the Neandertal geographic range. Many agree with Cartmill and Smith (2009) in noting that the 8- to 9-year-old subadult possesses a number of the derived Neandertal traits, including an “en-bombe” shaped cranial vault, an age-appropriate development of a continuous supraorbital torus, a suprainiac fossa, a characteristically Neandertal mastoid-juxtamastoid eminence configuration, and midsagittal facial prognathism, as well as a Neandertal-like infraorbital morphology and overall mandibular form. However, some have pointed to details of the vault and/or face that deviate from the classic European Neandertal pattern and appear more modern-like (Weidenreich, 1945; Minugh-Purvis and Lewandowski, 1994; Ritzman, 2005). Most recently, Glantz et al. (2009) have applied multivariate methods on continuous linear dimensions of the cranium and mandible and conclude that Teshik-Tash 1 is not typical of European Neandertal subadults. Similar arguments have been applied to the Middle Paleolithic associated subadult Uzbekistani material from the Obi-Rakhmat Grotto whose preserved teeth show clear Neandertal affinities (Bailey et al., 2008), while aspects of its highly fragmented cranium are argued to show some modern human characteristics (Glantz, 2010). However, as noted above, mtDNA sequences extracted from the Teshik-Tash remains are identical to those of other, undisputed Neandertals, and mtDNA recovered from postcranial remains at Okladnikov Cave located 2,000 km to the northeast of Teshik-Tash also possesses diagnostic Neandertal sequences (Krause et al., 2007).

In contrast to the differences of opinion regarding the morphological pattern of Teshik-Tash, the craniofacial anatomy of the Middle Paleolithic-associated individuals from the more recent levels at the Shanidar Cave site in the Zagros Mountains of Iraq (Shanidar 1 and 5) display the quintessential classic Neandertal morphological pattern (Trinkaus, 1983, 1984, 1995). However, there is minor variation in some features. For example, the most complete skull from this sample (Shanidar 1) displays less nuchal bunning compared to European

Neandertals. In addition, Trinkaus (1982) noted that the degree of frontal flattening combined with the pattern of parietal curvature in Shanidar 1 and 5 were unusual and could be the result of purposeful cranial deformation induced as subadults during growth based on well-understood mechanical procedures documented among some extant humans. Trinkaus further noted that this potential practice would have co-occurred with purposeful burial at Shanidar, marking important social behavioral patterns linked to those observed among early modern humans (see below). A subsequent reconstruction of portions of the Shanidar 5 cranial vault led Trinkaus and colleagues (Chech et al., 1999) to clarify that cultural cranial deformation for Shanidar 5 was unsupported, but that both Shanidar 1 and 5 nonetheless clearly have an unusual pattern of frontal midsagittal flatness. Interestingly, the earlier Shanidar 4 individual also shows this trait (Trinkaus et al., 1996).

Another chronologically later Neandertal sample from Amud (northern Israel) also shows the quintessential classic Neandertal morphological pattern, particularly in the well-preserved Amud 1 cranium and mandible (albeit, minus the midface; Figure 2.4) (Suzuki, 1970). As with the later Shanidar sample, Amud 1 has been argued to show regional variation compared to European Neandertals, particularly in its posterior cranial vault, which has little to no nuchal bunning and somewhat more rounding of the cranial vault in general (Cartmill and Smith, 2009). Multivariate analysis of its frontal bone has been argued to show similarities to the Levantine early modern sample (Simmons et al., 1991; Smith et al., 1995), while more recent frontal bone profile comparisons (Athreya, 2009) dispute this contention and argue instead that Amud 1 is more similar to Western European Neandertals than to other West Asian Neandertals; which, Athreya notes, was also originally concluded by Suzuki and Takai (1970; but see Arensburg and Belfer-Cohen, 1998). The Amud 7 infant (ca. 10 months of age) has been argued to show clear Neandertal characteristics in its craniofacial remains, most particularly in its elongated foramen magnum, pronounced superior medial pterygoid tubercle, and aspects of its mandibular symphysis (Rak et al., 1994).

While the 60–50 ka Kebara 2 individual lacks the diagnostically important cranium, it retains a fairly complete mandible that shows several clear Neandertal-derived features,



Figure 2.4. Lateral view of the Amud 1 cranium from Israel. From Cartmill and Smith (2009). Used with permission. © Matt Cartmill.

including a posterior position of the mental foramen, a horizontal-oval mandibular foramen configuration, a retromolar space, and a pronounced superior medial pterygoid tubercle (Tillier, 1991). However, it also shows a plesiomorphic level of corpus robusticity that clearly exceeds other Western Asian and coeval European Neandertals (Tillier, 1991; Dobson and Trinkaus, 2002; Tillier et al., 2003), providing another example of marked craniofacial variation evident in this region.

The craniofacial remains of the 2-year-old Mousterian-associated infant discovered in 1993 from the Dederiyeh Cave in northern Syria possess several features consistent with Neandertal affiliation, including an incipient suprainiac fossa and occipital torus, a relatively large nuchal plane, an elongated foramen magnum, a relatively tall zygomatic frontal process height relative to total zygomatic height, a prominent nasal bridge, several Neandertal mandibular symphysis characteristics, and a laterally positioned mandibular condyle (Dodo et al., 1998). The bony labyrinth in Dederiyeh 1 clearly shows the derived morphology found in virtually all Neandertals (Spoor et al., 2002, 2003) and is particularly important given that this trait is fully established in its morphology at very early stages of development, unlike many other craniofacial traits whose precise expression alters differentially throughout ontogeny (Tillier, 1998; Richards et al., 2003).

In addition to the regional variability noted in the Western Asian Neandertals relative to their broadly coeval European counterparts, important chronological variation occurs specifically within the Shanidar Middle Paleolithic Neandertal sample. Trinkaus (1983, 1984) has noted that the facial remains from the chronologically earlier sample (Shanidar 2 and 4) evince less midfacial prognathism than the later Shanidar 1 and 5 individuals (and European Neandertals), a greater degree of zygomatic angulation, rather than the more swept-back configuration in the later group, as well as an overall more robust facial configuration. These features in the earlier Shanidar 2 and 4 individuals are similar to the even earlier Zuttiyeh craniofacial remains discussed above. The question of chronological variation is particularly complicated by the current uncertainty regarding the dating of the Levantine Tabun C1 female skeleton. As discussed in greater detail below, she may have derived from levels as old as 180–170 ka, or alternatively may date to only 90 ka or even younger. Although the mid-face is incomplete, Trinkaus (1983) suggests that the degree of midfacial prognathism in Tabun C1 was likely less than that found in the later and more derived Shanidar 1 and 5 individuals and closer to the condition seen in the earlier and less derived Shanidar 2 and 4 faces. Her overall vault configuration appears somewhat more rounded than is typical for European Neandertals, along with little to no occipital bunning as in Amud 1. However, condylar and superior ramus features in the mandible of Tabun C1, while damaged, appear to show the derived configurations associated with typical Neandertals (Rak, 1998), and Hublin (1998) considers the occipito-mastoid region in Tabun C1 to be one of the most derived among all of the Levantine Neandertals. Moreover, the labyrinth morphology of Tabun C1 also shows the highly derived characteristics evident in the chronologically younger Neandertal specimens from Western and Southern Europe (Spoor et al., 2003). It would seem that craniofacially (as is evident from her postcranial skeleton, see above), Tabun C1 falls well into the derived Neandertal morphological pattern.

The isolated but well-preserved and largely complete Tabun C2 mandible (Figure 2.5), in contrast, presents a much more unresolved picture regarding its affinities, and it is a major problem in clarifying the picture of late human evolution in this region. While its attribution to level C at Tabun is unquestionable, making it older than the Skhul-Qafzeh sample (see below), it evinces a mosaic set of primitive or archaic features and modern attributes that has resulted in markedly different interpretations. On the archaic (and/or Neandertal) side, the mandible is quite long and robust overall with a large anterior dentition, a clear retromolar space according to most specialists, a pronounced superior medial pterygoid tubercle,

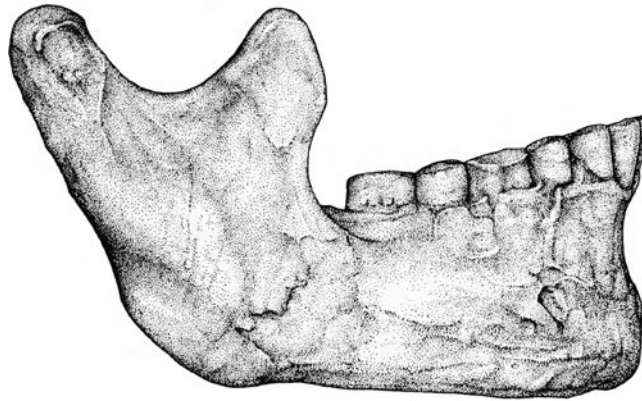


Figure 2.5. Lateral view of the Tabun C2 mandible. From Cartmill and Smith (2009). Used with permission. © Matt Cartmill.

a horizontal-oval mandibular foramen, a posterior position of the mental foramen that lies under the P_4/M_1 septum, and anterior-posterior dental proportions reflecting larger anterior teeth and smaller posterior ones. On the modern side, Tabun C2 has an essentially modern-like chin configuration with a basal projection at the symphysis, an incurvature above this projection associated with laterally positioned mental fossae, and anterior marginal tubercles, although it is important to note that portions of this area have been damaged and restored and that it differs in some details from the modern Skhul-Qafzeh configurations (see Stefan and Trinkaus, 1998). It also possesses a more medially placed condyle in which the mandibular notch crest is oriented laterally, and a symmetrical mandibular notch with its lowest extent located at midpoint between the coronoid process and the condyle. The last two modern features are emphasized by Rak (1998), who also questions the presence of the retromolar space in Tabun C2 as is usually defined (Franciscus and Trinkaus, 1995; Cartmill and Smith, 2009), arguing instead that it presents a non-homologous “pre-angular notch.” The Tabun C2 mandible, originally interpreted by McCown and Keith (1939) as deriving from a transitional population between Neandertals and modern humans, thus has in more recent years been seen as an early modern human (Vandermeersch, 1981; Bar-Yosef and Pilbeam, 1993; Rak, 1998), or as showing affinities in rather equal measure to both Neandertals and modern humans (Quam and Smith, 1998), or as a somewhat idiosyncratic specimen but one that essentially represents a Neandertal or other archaic Levantine population (Trinkaus, 1983, 1984, 1993b; Tillier, 1991; Stringer & Gamble, 1993; Schwartz & Tattersall, 1997).

Compared to the abundant Middle Paleolithic fossil human record in Western Asia, human skeletal remains from the early Upper Paleolithic in this region (all attributable to *Homo sapiens*) are meager. The earliest of these is the ca. 35 ka subadult burial from Ksar Akil, Lebanon (Bergman and Stringer, 1989), which has been lost, two frontals from Upper Paleolithic levels at Qafzeh, and fragmentary remains from Hayonim, Israel level D. Additional fragmentary material attributed to the “Aurignacian” is known from Kebara, el-Wad and Shukbah (McCown and Keith 1939), which has recently been relocated and is currently being reanalyzed (Trinkaus, personal communication). There is also an unpublished fragment of a human parietal from the Baradostian layer C of Shanidar Cave that has been recovered from the faunal remains (Trinkaus, personal communication). Isolated modern human remains from an MNI of four individuals, including two juveniles, are also known from Eshkaft-e Gavi, a cave located in the southern Zagros Mountains of Iran (Scott

and Marean, 2009). These include a mandibular molar, four cranial fragments, a clavicular diaphysis, a proximal metacarpal portion, a fragment of os coxae, the proximal diaphysis of a juvenile femur, and a patella. Scott and Marean (2009) note that while most of these elements could be Epi-Paleolithic in age, the juvenile mandibular molar clearly derives from the base of the cave's Upper Paleolithic sequence. Interestingly, Scott and Marean document that one of the pieces of frontal bone, the clavicle, the juvenile femur, and the patella all display clear evidence for intentional butchery in the form of stone-tool cutmarks, and along with a fragment of parietal bone, are also burned. More complete Upper Paleolithic remains from Israel at Ohalo 2 and Nahal Ein Gev 1 are also known, but these are unquestionably considerably later in time (see below).

In addition to such taxonomic and phylogenetic considerations, the craniofacial anatomy of the extensive Western Asian Late Pleistocene samples has figured prominently in a range of adaptive and behavioral issues. In his initial description of Shanidar 1, Stewart (1959) mentioned an unusually depressed internal nasal floor and subsequently described the same anatomy in Shanidar 2 (Stewart, 1961). The depressed internal nasal floor was also noted in Amud 1 by Suzuki (1970), who pointed out its presence in several European Neandertals, and again by Stewart (1977), who posited that facial size in modern humans was too reduced to accommodate the characteristic Neandertal nasal floor depression. While this trait has since been mentioned frequently as a Neandertal autapomorphy (Stringer and Trinkaus, 1981; Stringer, 1983; Trinkaus, 1983; Stringer et al., 1984; Hublin, 1991; Arsuaga et al., 1997b, 1999a), some have argued that the more capacious internal nasal dimensions of Neandertals are instead tied to adaptive factors. These include climatic and/or respiratory physiological factors such as cerebral thermoregulation, body core heat shedding due to vigorous activity in cold climates to prohibit sweating and hypothermia, upper respiratory demands in cold environments, and the need to facilitate the physiological demands of a large body mass (e.g., Coon, 1962; Trinkaus, 1987a; Dean, 1988; Franciscus and Trinkaus, 1988; Churchill et al., 1999; Rosas et al., 2006). A recent survey (Franciscus, 2003) found that the depressed nasal floor was also present in Shanidar 5 and the Tabun B1 subadult but not in Tabun C1, which has a shallower configuration. Moreover, Skhül 4 and the Qafzeh 4 subadult both have a depressed nasal floor, while Qafzeh 9 and the Qafzeh 11 subadult, in contrast, have a completely flat, non-depressed floor, and Qafzeh 6, like Tabun C1 shows an intermediate configuration. These observations in Levantine early modern humans and Neandertals coupled with broader comparisons to both fossil *Homo* and extant human samples do not support cold-climate and activity-related thermal adaptation arguments as an explanation for the high frequency of nasal floor depression in Neandertals, and their lower frequencies in other groups, and are more likely related to some combination of overall facial size and projection and stochastically derived populational differences in fetal nasofacial growth patterns.

Non-dietary use of the anterior teeth, or the use of teeth as tools in Neandertals, and ideas regarding a significant decrease in such paramasticatory behavior among anatomically modern humans have also been substantially influenced by craniofacial and dental observations in the Western Asian Late Pleistocene samples. Trinkaus (1983, 1984) noted differences in both the size and wear patterns evident in the anterior dentitions between the Skhül-Qafzeh sample and Neandertals such as Shanidar 1, 3, 4, and 5. These observations were also tied to the shifts in midfacial prognathism within the Western Asian Neandertals in which the later Shanidar 1 and 5 individuals showed a derived posterior migration of the zygomatic region, while maintaining the more archaic anterior positioning of the dentition. Under conditions of frequent paramasticatory behavior, the posteriorly positioned zygomatics were seen as less effective in absorbing the masticatory stresses directed superoposteriorly through the facial skeleton. The derived shift to a flattened or anteriorly inflated maxilla (one lacking

a canine fossa; see note #2) in the later Neandertals was seen as a mechanism to minimize stress concentrations in the infraorbital region and more effectively transmit forces through the nasofacial skeleton and up through the supraorbital and frontal regions (Heim, 1976; Smith, 1983; Trinkaus, 1984). These ideas generated a spate of later studies both supporting a significant biomechanical interpretation for the derived Neandertal face and its difference from modern humans (Rak, 1986; Demes, 1987; Trinkaus, 1987b; Smith and Paquette, 1989; Spencer and Demes, 1993) and studies downplaying biomechanics in this regard (Antón, 1990, 1994; Couture, 1993; Dobson and Trinkaus, 2002; O'Connor et al., 2005; Clement et al., in press), in particular ideas related to high anterior tooth occlusal loading. Moreover, in recent years evidence has steadily accumulated regarding the importance of neutral evolutionary processes over adaptive ones in shaping Neandertal craniofacial morphology (e.g., Antón, 1994; Maureille and Houët, 1998; Hublin, 1998, 2009; Franciscus, 2002, 2003; O'Connor et al., 2005; Weaver et al., 2007, 2008; Holton and Franciscus, 2008). Clearly, directional selection on Neandertal facial form in response to both biomechanical and especially climatic factors occurred as it does to variable degrees in most populations, including those of early moderns. However, these adaptive factors were likely *secondary* causal mechanisms overlying, accommodating, and being constrained by the more *primary* stochastic patterns that emerged and crystallized during the Late Pleistocene.

Another key behavioral issue impacted by Western Asian fossil craniofacial remains has centered on the evolution of spoken language, its role in defining human uniqueness, and longstanding arguments for and against modern human-like speech capacities in Neandertals (Schepartz, 1993). The discovery of the Levantine Kebara 2 adult male Neandertal marked the first time in human paleontology that a hyoid bone had been recovered (Arensburg et al., 1989) and, given its primary function as an anchoring structure for the root of the tongue and positional relationship to the larynx, or voice box, it generated considerable discussion and debate. Arensburg et al. (1989, 1990) argued that the overall size and shape of the bone, as well as its positional relationship to the larynx in Kebara 2, was essentially like that of modern humans, indicating the capacity for spoken language. These conclusions were challenged by P. Lieberman and colleagues (Lieberman et al., 1992; Lieberman, 1994), who questioned whether the morphology and measurements of the hyoid bone were, in fact, accurate reflections of the position of the larynx relative to speech production. Subsequent hyoid remains from a 43 ka Neandertal from Asturias, Spain (Rodríguez et al., 2003), and two Middle Pleistocene individuals from the Sima de los Huesos, Atapuerca, Spain (Martínez et al., 2008), have confirmed an essentially modern human-like hyoid morphological pattern, one that was likely present in the last common ancestor of modern humans and Neandertals, and perhaps even earlier (Martínez et al., 2008). Whether or not the hyoid bone morphological similarities to extant modern humans actually reflect comparable speech capacities in earlier *Homo* nonetheless remains unresolved.

Trauma and Behavioral Inferences

While there is abundant, well-documented evidence for human trauma since the Middle Pleistocene (e.g., Berger and Trinkaus, 1995; Trinkaus et al., 2006; Shang and Trinkaus, 2008), it is only in more recent time periods that evidence for the actual causality of trauma is both unambiguous and attributable to factors other than those involving accidental injury, or injury secondary to everyday subsistence. For example, the earliest widely accepted instance of death attributable to interpersonal (or intergroup) violence clearly involving weaponry comes from the Nubian site of Jebel Sahaba dated to ca. 14 ka BP (Anderson, 1968; Wendorf, 1968), and further well-documented instances derive from later Mesolithic sites

(Freyer, 1997). In light of this, Western Asia has produced some of the earliest, albeit debated, instances of traumatic injuries linked to cause of death and injuries possibly deriving from some form of interpersonal violence.

The possibility of a weapon-inflicted lesion in a Mousterian-associated modern human adult male from Skhül Cave was first noted by McCown and Keith (1939), who described a rectangular opening penetrating through the head of the left femur and acetabulum of Skhül 9, and on the basis of a lack of a recovered weapon armature, argued that it had been made by a wooden spear that had subsequently disintegrated. A second, shallower “lesion” also penetrated the ilium above the superoposterior margin of the acetabulum in this Levantine early modern individual now dated to 120–90 ka (Stringer et al., 1989; Mercier et al., 1993). A number of observations regarding the details of the femur and pelvic bone damage to Skhül 9, contextual aspects of the burial, as well as stabbing/thrusting force ballistics considerations detailed in Churchill et al. (2009) argue against McCown and Keith’s conclusions regarding perimortem interpersonal violence and instead are more consistent with postmortem excavation damage.

A far more compelling case of traumatic injury linked to cause of death, and possibly deriving from some form of interpersonal violence among hominins in the later Pleistocene of Western Asia, derives from the adult male Shanidar 3 individual, part of the large Neandertal assemblage excavated between 1953 and 1960 from Shanidar Cave, in the Zagros Mountains of northeastern Iraq (Solecki, 1963; Stewart, 1977; Trinkaus, 1983). The well-preserved thoracic skeleton of Shanidar 3 exhibits a partially healed penetrating injury to the cranial aspect of the left 9th rib, suggesting a possible resultant pneumothorax; he likely survived for somewhere between 2 weeks and about 2 months after receiving the injury prior to death (Churchill et al., 2009). This injury, originally described by Stewart (1969, 1977) and Trinkaus (1983; Trinkaus and Zimmerman, 1982), appears to represent sharp force trauma from a lithic point or blade and has long led to guarded speculation concerning interpersonal violence among the Shanidar Neandertals (Solecki, 1960; Stewart, 1969, 1977; Trinkaus and Zimmerman, 1982; Trinkaus, 1983; Shea, 1990; Holdaway, 1990; Solecki, 1992), or possibly interspecific violence between Neandertals and early modern humans (Roper, 1969).

More recently, stemming from additional observations on details of the wound (Franciscus and Churchill, 2002) and an experimental approach to deciphering the wound etiology (Churchill et al., 2009), this question has been further explored. Based on controlled stabs into pig carcass thoraces with replicas of Mousterian and Levallois points using high and low kinetic energy conditions designed to replicate forces associated with thrusting spear versus long-range projectile weapon systems, Churchill et al. (2009) concluded that the precise morphology of the lesion in Shanidar 3 is most consistent with the rib injuries produced in the pigs by a low-mass, low kinetic energy projectile weapon. Moreover, study of goat ribs subjected primarily to high kinetic energy (thrusting) stabs in an independent experiment (Shea et al., 2001) by Churchill and colleagues revealed consistent differences in damage patterns between the two conditions. Churchill and colleagues noted that while accidental injury or attack with a thrusting spear or knife cannot absolutely be ruled out in the case of Shanidar 3, the experimental evidence pointing to a low-mass, low kinetic energy projectile weapon re-raised the possibility of interspecific violence between Neandertals and early modern humans at this time in Southwest Asia since there is no evidence for projectile weapon usage by Neandertals.

Trinkaus and Buzhilova (2010) have challenged the possibility of regional sympatry of Shanidar 3 with early modern humans in Western Asia as argued by Churchill et al. (2009), and also note that while Middle Paleolithic spears generally had relatively thick lithic points (Shea, 2006), thinner tools capable of producing the Shanidar 3 injury are present in the

Shanidar (and Southwest Asian) Middle Paleolithic (Skinner, 1965). Consequently, they see no basis for inferring that individuals responsible for the Shanidar 3 injury were other than Neandertals.³ Such disagreements notwithstanding, Western Asia, in the specific case of Shanidar 3, remains a compelling case for the region producing the earliest trauma likely associated with death and likely attributable to some form of hominin interpersonal violence. Indeed, the only other instance of known cause of death, prior to the very late Upper Paleolithic, which also involved a likely interpersonal violent demise is the Gravettian-associated individual from Sunghir 1 in northern European Russia (Trinkaus and Buzhilova, 2010) dated to 27–26 ¹⁴C ka BP (Kuzmin et al., 2004; Dobrovolskaya et al., 2012).

Burials

The extensive sample of human skeletal remains deriving from Western Asia that has proven exceptionally important to our current understanding of the origin(s) of modern humans is, to a great extent, the direct result of the differential taphonomic survivorship that purposeful burial affords to skeletal remains. Moreover, human mortuary practices, at some point in time, became part of a larger framework of “symbolic” capacity (Pettitt, 2011), which itself has been used by some as a major defining characteristic of modern humans (e.g., Chase and Dibble, 1987; Bar-Yosef, 2002; Hovers et al., 2003; Hensilwood and Marean, 2003; Belfer-Cohen and Hovers, 2010). While there is scattered and ambiguous evidence for various types of hominin carcass processing during the Lower, Middle, and Later Pleistocene in Africa, Eurasia, and Asia (Pettitt, 2011), and possibly some form of long-term anthropogenically derived body caching at the Middle Pleistocene Sima de los Huesos site at Atapuerca, N. Spain (Arsuaga et al., 1997a; Garcia et al., 1997; Andrews and Fernandez-Jalvo, 1997), evidence for purposeful human inhumation first appears in the Levant of Western Asia.

While, as noted above, it is widely accepted that anatomically modern (or nearly modern) humans appear first in Africa in Ethiopia at Omo-Kibish at ca. 195 ka and Herto at ca. 160 ka (Day and Stringer, 1982; White et al., 2003; Clark et al., 2003; McDougall et al., 2005), neither of these shows evidence for purposeful burial. This is also true for the ca. 100 ka modern or near-modern human isolated remains from Klasies River Mouth (Singer and Wymer, 1982; Rightmire and Deacon, 2001), even if they, like the Herto remains, show some evidence for cutmark damage. The earliest evidence for purposeful inhumation that is widely accepted⁴ to date comes from the Middle Paleolithic sites of Skhül, Qafzeh, and Tabun in the Levant, and Shanidar in the Zagros region of Iraq (Table 2.1).

At least ten individuals appear to have been buried at Mugharet-es-Skhül (Mount Carmel, Israel) between 130 and 100 ka based on ESR, U-series, and TL dating (Mercier et al., 1993; Grün et al., 2005). While four of these early modern human individuals (1, 4, 5, and 9) were burials in the strict sense according to Pettitt (2011), having been placed in artificially excavated grave cuttings, all ten can be seen as purposeful inhumations in a relatively discrete time period, although it is possible that Skhül 9 is older than the rest of the sample (Grün et al., 2005). Coupled with other observations, and dependent on the unresolved dating of the Tabun C1 Neandertal individual (see below), this has suggested the possibility that Skhül 9 may, in fact, represent the earliest known case of intentional hominin burial (Stringer, 1998). Interestingly, there remains a question regarding the burial proximity of the Skhül 10 child, who was found close to the head of the Skhül 7 adult female, as to whether these represent two separate inhumations, or a single burial event. While this is probably unresolvable, if the latter is correct, it would represent the earliest known example of an adult buried with a child, a dynamic that is also possible at Qafzeh and Tabun (see below)

Table 2.1. Early Middle Paleolithic to early Upper Paleolithic individuals with evidence of purposeful inhumation.^a

Early Middle Paleolithic (120–90 ka BP)		
Qafzeh 3	adult	W. Asia
Qafzeh 6	adult male	W. Asia
Qafzeh 7	adult	W. Asia
Qafzeh 8	adult	W. Asia
Qafzeh 9	adult female	W. Asia
Qafzeh 10	child	W. Asia
Qafzeh 11	adolescent	W. Asia
Qafzeh 12	child	W. Asia
Qafzeh 13	infant	W. Asia
Qafzeh 15	child	W. Asia
Qafzeh 21	child	W. Asia
Qafzeh 22	child	W. Asia
Shanidar 4	adult male	W. Asia
Shanidar 6	adult female	W. Asia
Shanidar 7	infant	W. Asia
Shanidar 8	adult female	W. Asia
Shanidar 9	infant	W. Asia
Skhül 1	child	W. Asia
Skhül 2	adult	W. Asia
Skhül 3	adult male	W. Asia
Skhül 4	adult male	W. Asia
Skhül 5	adult male	W. Asia
Skhül 6	adult male	W. Asia
Skhül 7	adult female	W. Asia
Skhül 8	child	W. Asia
Skhül 9	adult male	W. Asia
Skhül 10	child male	W. Asia
Early Middle Paleolithic (120–90 ka BP) or Later Middle/Early Upper Paleolithic (70–35 ka BP)		
Tabun C1 ^b	adult female	W. Asia
Later Middle/Early Upper Paleolithic (70–35 ka BP)		
Amud 1	adult male	W. Asia
Amud 7	infant	W. Asia
Amud 9 ^c	adult	W. Asia
La Chapelle-aux-Saints 1	adult male	W. Europe
Dederiyeh 1	infant	W. Asia
Dederiyeh 2	infant	W. Asia
Feldhofer 1	adult male	W. Europe
La Ferrassie 1	adult male	W. Europe
La Ferrassie 2	adult female	W. Europe
La Ferrassie 3	child	W. Europe

Table 2.1. (Continued)

La Ferrassie 4b	infant	W. Europe
La Ferrassie 5	fetus	W. Europe
La Ferrassie 6	child	W. Europe
La Ferrassie 8	infant	W. Europe
Kebara 1	infant	W. Asia
Kebara 2	adult male	W. Asia
Kiik-Koba 1	adult male	E. Europe
Kiik-Koba 2	infant	E. Europe
Mezmaiskaya 1	infant	E. Europe
Le Moustier 1	adolescent	W. Europe
Le Moustier 2	infant	W. Europe
Nazlet Khater 1a	adult male	N. African
Nazlet Khater 1b	fetus	N. Africa
Nazlet Khater 2	adult male	N. Africa
La Quina 5	adult	W. Europe
Le Régourdou 1	adult	W. Europe
Roc de Marsal 1 ^d	infant	W. Europe
Saint-Césaire 1	adult	W. Europe
Shanidar 1 ?	adult male	W. Asia
Shanidar 3 ?	adult male	W. Asia
Spy 1	adult	W. Europe
Spy 2	adult	W. Europe
Teshik-Tash 1 ?	child	W. Asia
Taramsa 1	child	N. Africa
Zaskalnaya 1	infant	E. Europe
Zaskalnaya 2	infant	E. Europe
Zaskalnaya 3	infant	E. Europe

^a Inclusion based on listing in Zilhão (2005), unless otherwise indicated. The broad chronological divisions and their sample inclusions also follows Zilhão (2005). The inclusion of the European sites highlights the difference between the earliest time periods prior to the later Middle/early Upper Paleolithic (before 70 ka BP), which is dominated by burials from W. Asia compared to the more geographically variable occurrence of burials after 70 ka BP. Age classes as defined by Zilhão are: up to 3 years (fetus and infant), up to 12 years (child), up to 15 years (adolescent), 16 years and older (adult). For adults, sex attribution is provided only in cases where there is reasonable consensus.

^b The geological age of Tabun C1 is unclear, although a number of workers agree that it belongs with the early Middle Paleolithic group (120–90 ka, or perhaps even earlier); see text for details. Although the skeleton's exact age is unknown, there is broad consensus regarding its Neandertal taxonomic designation and female sex.

^c Western Asian individuals added based on Pettitt (2011).

^d The Roc de Marsal Neandertal infant, long considered a secure burial due primarily to its skeletal intactness and evidence for an excavated pit, has been challenged based on recent work at the site (Sandgathe et al., 2011).

?= Individuals listed as purposeful interments in Zilhão (2005) that are not considered valid by Pettitt (2011).

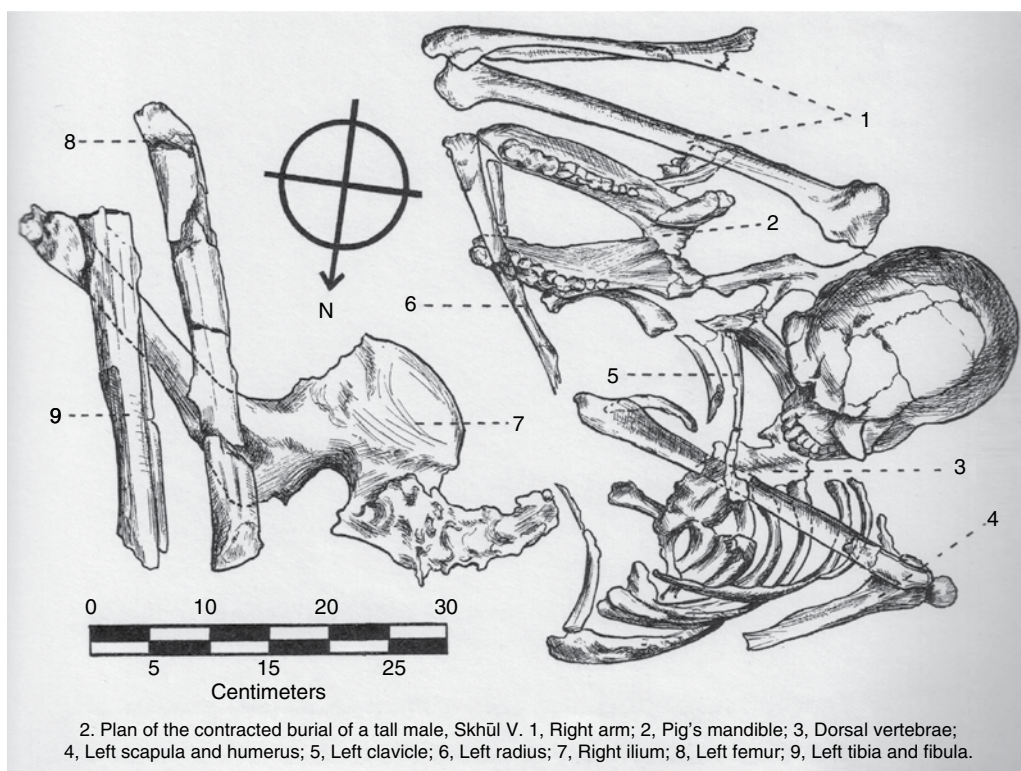


Figure 2.6. In situ burial plan of Skhül 5 from Mt. Carmel, Israel. From Garrod and Bate (1937). Used with the permission of Oxford University Press.

but is otherwise not documented until ca. 80–75 ka later (Pettitt, 2011), unless one allows for the possibility at Shanidar Cave also (see below). It is also noteworthy that a large boar mandible was included in the Skhül 5 burial (Figure 2.6), positioned between his left forearm and right upper arm, constituting perhaps the earliest known example of deliberate grave inclusion (Pettitt, 2011). Moreover, red pigmented materials from the B layer at Skhül have been interpreted as being used in both functional and symbolic activities (d’Errico et al., 2010). It is also possible that mollusk shells interpreted as personal adornment were linked with some of the Skhül burials, although a definitive association cannot be made (Bar-Yosef Mayer et al., 2009).

The remains of seven adults, nine subadults, and a number of isolated remains representing early modern humans were recovered from the site of Qafzeh (near Nazareth, Israel) dated to 100–90 ka based on ESR and TL dating (Schwarcz et al., 1988; Valladas et al., 1988). At least six of the individuals (8, 9, 10, 11, 13, and 15) are the result of formal burials (Vandermeersch, 1981; Belfer-Cohen and Hovers, 1992), and it is possible that the incomplete remains of three others (3, 6, and 7) may have been interred collectively, although this cannot be confirmed (Defleur, 1993). The Qafzeh 9 adult and 10 subadult have been interpreted as a double burial, possibly of mother and child (Bar-Yosef and Vandermeersch, 1993), and were found in association with several ochre fragments. The Qafzeh 11 burial is particularly rich in apparent associated grave goods including stone blocks lining the grave, a large red deer antler and frontal bone near the child’s head and hands, an abundance of red ochre in the grave, and a large block apparently used to cover the grave (Vandermeersch,

1981; Belfer-Cohen and Hovers, 1992). Collectively, this makes the Qafzeh 11 burial the most elaborate known from Middle Paleolithic contexts according to some (see Pettitt, 2011), although it can be reasonably argued that the particular acceptance or rejection of animal bones as actual grave goods is not necessarily consistent across all early modern human and Neandertal interment contexts. All of the Qafzeh individuals derived from the same stratum, except for the Qafzeh 11 subadult who was found in a lower level, and a variety of evidence suggests that the inhumations, as for the Skhul remains, likely occurred in a relatively discrete time period as opposed to separate time transgressive episodes (Pettitt, 2011). Additional symbolic material recovered from Qafzeh includes an incised cortical flake and several marine shells originating from the Mediterranean Sea shore ca. 35 km from the site showing traces of ochre staining and having been strung (Bar-Yosef Mayer et al., 2009).

The fossils excavated in 1932 by Dorothy Garrod's team from Mughareh et-Tabun, Mount Carmel, Israel (McCown and Keith, 1939) included an adult Neandertal female, Tabun C1, which is recognized as a purposeful interment (Garrod and Bate, 1937; Defleur, 1993; Zilhão, 2005; Pettitt, 2011). Intriguingly, Garrod described an association of the Tabun C1 woman with the remains of a neonate found near her humerus in a 1933 communication (see Bar-Yosef and Callander, 1999). All evidence suggests that either Garrod was mistaken on this point or that the fragile bones of the neonate did not survive later excavation from the burial block. While Bar-Yosef and Callander favor the latter, the question is likely unresolvable. The Tabun C1 female, as Garrod herself first surmised, is widely recognized as a Neandertal (unlike the Tabun C2 mandible whose taxonomic affinity, as discussed above, is ambiguous); however, her geochronological age is unclear. Even at the time of discovery in 1932, Garrod noted that there was uncertainty in determining whether Tabun C1 was deposited during the formation of level C or instead derived from an intrusive interment from the overlying B level (see Bar-Yosef and Callander, 1999). Relevant to the perspective that Tabun C1's association with the older C level is correct (Kaufman, 2002; Zilhão, 2005), Mercier et al. (1995) have reported TL dates for that level of 180–170 ka, and more recently, Mercier and Valladas (2003) report two TL-based average date clusters for this level (one at ca. 178 ka, and another at 134 ka). Moreover, the younger of these two date clusters corresponds to ESR ages obtained for the dental material of the Tabun C1 skeleton of 143 and 112 ka depending on early or late uptake models (Grün and Stringer, 2000). For some (e.g., Zilhão, 2005), these results suggest that the Tabun C1 Neandertal interment, not the early anatomically modern Skhul 9 inhumation, represents the earliest intentional burial, and thus argues against the notion that Neandertal funerary practices were an imitative behavioral adoption from modern humans as suggested by Hublin (2000). However, Stringer (2006) notes that current dating, in fact, only has the resolution to place the Skhul, Qafzeh, and Tabun burials as approximately contemporaneous, thus making it impossible to ascertain which populations may have first originated the practice of purposeful burial. It is also worth considering whether arguments that focus on first burial occurrence and to which group the practice was diffused ignore the idea that the presence of burial in both groups at about the same time indicates that both had the same general level and nature of social bonding that is inherent to the behavior. Given the lack of evidence for grave goods associated with the Tabun C1 Neandertal inhumation, however, it can still be argued that the oldest known "symbolic" burials are those of early modern humans at Skhul and Qafzeh. For those who accept the archaeological arguments for the latter, it would appear that despite the possession of Middle Paleolithic technology, crucial aspects of modern human behavior were nonetheless present in the Levant prior to 100 ka and point to the likely multifaceted and mosaic nature of the emergence of modern behavior (Belfer-Cohen and Hovers, 2010).

At least four and perhaps as many as seven of the ten partial Neandertal skeletons⁵ excavated by Ralph Solecki between 1953 and 1960 at the Iraqi Kurdistan site of Shanidar Cave

show evidence for purposeful inhumation (Zilhão and Trinkaus, 2002; Zilhão, 2005; Pettitt, 2011). Five of these partial skeletons (4, 6, 8, 7, and 9) derive from levels whose precise geochronological ages cannot be determined, but they are possibly old enough to be considered in the early group of burials discussed above (Solecki, 1963; Trinkaus, 1983, 1995; Zilhão, 2005; Cowgill et al., 2007). Perhaps of greatest significance is the apparent sequential series of burials in which the Shanidar 9 infant was buried first, followed by two adult females (6 and 8), and then the adult male Shanidar 4 individual; all are in close proximity, suggesting that they were interred in a relatively narrow time period. Whether or not it was characteristic of the group overall, Pettitt (2011) assesses that at least this aggregate of Shanidar burials can be regarded as a place of multiple interment. Despite tremendous paleoanthropological interest and subsequent debate stemming from Solecki's argument that flowers had been included with the Shanidar 4 burial (Solecki, 1972), there appears to be very little current support for this interpretation. Indeed, there seems to be no clear evidence for any form of funerary practice (including grave goods) at Shanidar beyond purposeful inhumation (Pettitt, 2011).

In addition to the earliest burials, all from Western Asia discussed so far, there are additional occurrences from this region that date to younger than ca. 70 ka, albeit fewer in number, and in some cases with disagreement over burial genuineness (Table 2.1). The Shanidar assemblage includes two individuals (1 and 3) most likely deriving from MIS 3 based on a number of considerations (Trinkaus, 1983; Cowgill et al., 2007) that are considered to be burials by Zilhão (2005), but there is evidence that these were instead in situ deaths by rockfalls in the cave and not burials per se (Pettitt, 2011). Similarly, the remains of the Teshik-Tash Neandertal child from southeastern Uzbekistan (Okladnikov, 1949; Movius, 1953), long argued to be evidence for intentional burial and also symbolic behavior (in the form of ibex horns arranged to form a circle around the "burial"), lack key signatures of purposeful inhumation and are instead consistent with a variety of features found in carnivore assemblages (Pettitt, 2011).

From the highly fragmented and sparse sample of up to sixteen Neandertal individuals recovered from the Middle Paleolithic levels in Amud Cave (northern Israel) in the 1960s and early 1990s (Suzuki and Takai, 1970; Rak et al., 1994; Hovers et al., 1995), three individuals provide secure evidence that they were intentionally buried: two adults (1 and 9), and an infant (7). In addition to being a compelling case for intentional interment, the Amud 7 infant was also associated with a complete maxilla from a red deer positioned at the infant's pelvis. Pettitt (2011), noting that this particular taxon (*C. elaphus*) is otherwise represented only by isolated teeth, emphasizes the similarity to the early modern human burials of Skhül 5 and Qafzeh 11, which, as discussed above, were also associated with a single faunal cranial element that was not intrusive from outside of the burial space.

Excavations at the site of Kebara Cave (Mount Carmel, northwestern Israel) have resulted in a large number of human remains associated with a Mousterian archaeological context from excavations conducted in 1951–1965 and 1982–1990 (Tillier et al., 2003). While many of these are fragmentary and isolated remains from several individuals, two partial skeletons dated to ca. 60–50 ka based on radiocarbon, TL, and ESR dating are undoubted purposeful interments (Tillier et al., 2003; Pettitt, 2011). The Kebara 2 (KM2) adult male (Bar-Yosef and Vandermeersch, 1991; Figure 2.7) preserves virtually all of the upper torso, upper limbs, hands, hemipelvis, and partial left femur and is notable for the absence of the cranium, even though the mandible, hyoid bone, right upper third molar, and complete cervical vertebrae constituting the neck were found in anatomical position. These and other considerations led those who excavated and analyzed the remains to conclude that the cranium was removed purposefully at some later point after the decay of the atlanto-occipital ligaments, which would document the first case of human intervention in a primary burial recorded in a Middle Paleolithic context (Tillier et al., 2003). However, as detailed by Pettitt (2011), the

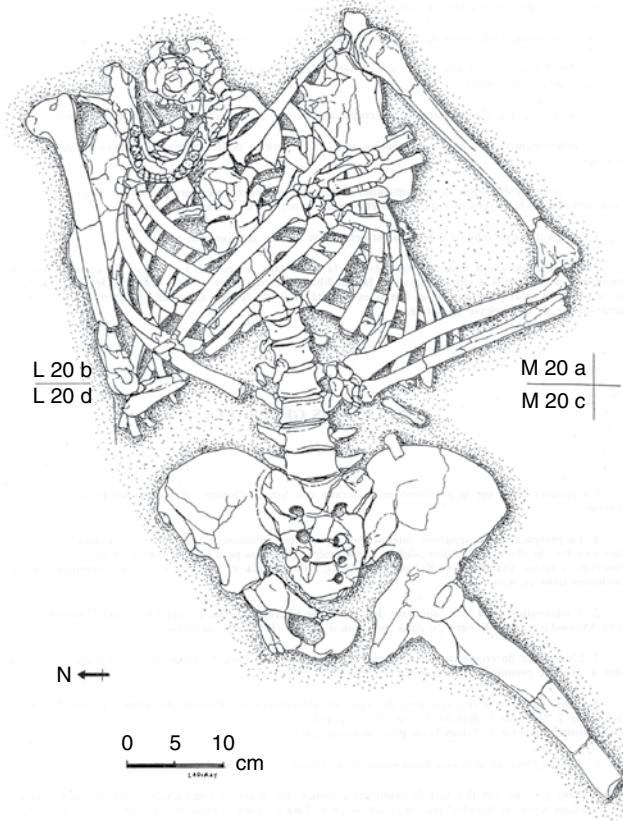


Figure 2.7. In situ burial plan of the Kebara 2 burial from Israel. Copyright of the Kebara Archives. From Tillier et al. (1991). Used with permission. © Kebara Archives.

excavators have more recently considered that taphonomic erosional processes related to the fact that the burial was originally positioned at an incline with the head at the highest level likely account for its absence without the need to invoke human manipulation. The well-preserved remains of the Kebara 1 (KMH1) infant found in the mid-1960s (Smith and Arensburg, 1977), and more recently restudied (Tillier et al., 2003), were recovered from a small spatial area that also contained three stones and a *Rhinoceros* tooth. While the evidence for purposeful inhumation is widely accepted, there seem to be no compelling reasons to interpret the stones and tooth as grave goods. Stones and fragmented faunal elements were also found with Kebara 2 and interpreted as part of the existing matrix into which the grave was cut to inter the remains (Bar-Yosef et al., 1992). These do not appear to rise to the level of symbolic potentiality noted for the Amud 7 Neandertal infant and the early modern human burials of Skhül 5 and Qafzeh 11 discussed above.

Rounding out the Western Asian later Middle Paleolithic (70–35 ka) interments are the two infant Neandertal burials from Dederiyeh Cave in northwestern Syria (Akazawa and Muheson, 2002; Akazawa et al., 2002a, 2002b). Dederiyeh 1 is a well-preserved, highly articulated, and nearly complete skeleton that was ca. 2 years of age at death. It was positioned in the grave lying on its back, with its legs flexed and its arms extended, and was clearly purposefully interred (Dodo et al., 1998). Pettitt (2011) notes that a roughly rectangular stone slab was found next to the cranium on which the head was possibly originally laid, and

the infant also had a small triangular piece of flint lying on its thorax; besides these features, the sediment around the skeleton was sterile. Dederiyeh 2 is a less completely preserved skeleton also ca. 2 years of age at death. Unlike the Dederiyeh 1 burial, the sediment around Dederiyeh 2 contained a large amount of lithic débitage and numerous faunal bone fragments; it also contained a large piece of a tortoise shell. The partial skeleton elements of Dederiyeh 2 found in its well-defined burial pit were not in articulation, and most of the axial body is missing. Based on these and other observations, Pettitt (2002, 2011) has speculated that the infant was originally deposited, and likely defleshed, at another site prior to being subsequently gathered up and interred in its eventual find location.

Western Asia has thus produced the majority of buried individuals known from Middle Paleolithic contexts in general, and for the earlier portion of this period (120–90 ka) Western Asia is the exclusive source for intentional interments. Interestingly, following a hiatus of no known burials anywhere between ca. 35 and 28 ka, numerous burials (as many as sixty-eight individuals from twenty different sites following Zilhão, 2005) are known from the period 27–20 ka deriving mostly from western, central, and eastern portions of Europe, and none deriving from Western Asia. This dearth of later burials in Western Asia continues into the late Upper Paleolithic with only two known Israeli cases (Ohalo 2, an adult male dated to 19 ka, and the approximately coeval Nahal Ein Gev 1 burial of an adult female), perhaps reflecting an off-site burial preference norm at this time, at least for the Levant (Spiers et al., 2004). It is only during the later Near Eastern Natufian period (ca. 13,000–10,300 ka) that burials, having apparently begun in the Near East more than 100,000 years earlier, again abound, with over four hundred documented interments (Pettitt, 2011).

Summary

Western Asia, especially the extensive and well-preserved human fossil record from Southwestern Asia, has long played a pivotal role in our understanding of Late Pleistocene human evolution and, in particular, our current understanding of the origin(s) of modern humans. Western Asia was the geographical corridor through which modern humans expanded into Europe and East Asia and is likely the region in which most of the recently documented gene flow between these expanding modern human populations and Neandertals occurred. The practice of intentional burial in this region by both Neandertals and early modern humans has produced an unmatched human paleontological record for this time period, even if the precise beginnings and attendant behavioral meanings surrounding human interment are currently unresolved. The degree of within and between sample morphological variability and mosaicism for Neandertals and early modern humans in this region is marked. This pattern of mosaicism, evident in the early days of discovery in the 1920–1930s, has been confirmed by the many subsequent finds, including those that have come to light since publication of the 1984 *Origins of Modern Humans* volume. Both adaptive and non-adaptive or neutral processes were likely at play in this key geographical corridor as this mosaic pattern of morphology unfolded, and ongoing work will continue to refine our understanding of these processes.

The Western Asian record reviewed here has also provided a considerable amount of empirical data that has been brought to bear on key biobehavioral issues in the Late Pleistocene, including early evidence for interpersonal violence, the evolutionary trajectory of human birthing patterns, speech capacity, biobehavioral response to climatic/ecological variation, activity and mobility patterns, techno-culture/somatic interaction, and contrasting ideas regarding the emergence of “symbolic” capacity within the larger framework of

“modernity.” The incorporation of genetic data and analyses into the mix in recent years—a major shift since the 1984 *Origins of Modern Humans* volume—has also augmented the substantial Western Asian paleontological and archaeological records for this pivotal time period in human evolution, and it is exciting to imagine what new refinements and discoveries await us in the coming years.

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Notes

1. While the manual phalanx from Denisova yielded mitochondrial and nuclear DNA sequences unseen in other ancient hominins, Susanna Sawyer and colleagues announced at the 2012 European Society for the Study of Human Evolution Meetings that a pedal phalanx from Denisova yielded Neandertal-like nuclear DNA. This means that either Denisova is at the margins of both the Neandertal and “Denisovan” ranges, or alternatively, that Neandertals were more genetically diverse than previously recognized.
2. The infraorbital surface topography of Neandertals, long characterized discretely as uniquely inflated or “puffy,” has not held up to detailed 3D geometric morphometric assessment (see Maddux and Franciscus, 2009; Maddux, 2011). This trait is shared with other relatively large-faced *Homo* individuals including those predating the Neandertal lineage. Uniquely parasagittally aligned infraorbital surfaces, in contrast, should still be seen as a derived Neandertal trait.
3. We note that attribution to *either* Neandertals or modern humans in this regard does not, in our view, automatically confer or suggest any inherently greater proclivity for, or frequency of, inter-personal aggression or violence in one group over that of the other group.
4. While opinions regarding the number of actual cases of purposeful inhumation within and across the range of Middle Paleolithic sites vary among researchers, very few workers have challenged the existence of Middle Paleolithic burials entirely as advanced by Gargett (1989, 1999).
5. Recent analysis of the faunal remains from Shanidar Cave has identified a hominin distal tibia, fibula, first metatarsal, and two tarsals deriving from a 1- to 2-year-old infant possessing Neandertal affinities that originated from the lowest hominin-bearing levels of the Middle Paleolithic sequence. These have been designated as Shanidar 10 (Cowgill et al., 2007) adding to the original nine individuals described in detail by Trinkaus (1983).

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Chapter 3

A River Runs through It: Modern Human Origins in East Asia

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Research on the origin of modern humans has generally focused on the western part of the Old World, specifically on Europe and the Levant, where a rich and steadily accumulating record of human fossils from the late Pleistocene has been known for over a hundred years. The leading hypotheses about modern human origins, “Multiregional Evolution” (Wolpoff et al., 1984) and “Recent Out of Africa” (Stringer and Andrews, 1988) have long been debated, especially in Europe and the Near East, where they generally have received the most attention and scrutiny. Interestingly, the issue has always been much less contentious at *another* geographical edge of the Pleistocene human range, namely East Asia, particularly China, which has produced the most abundant fossil record for human evolution in the eastern part of the Old World.

Specifically, the question is whether the succession of earlier human populations by later ones all over the Old World was due to (1) a gradual evolutionary process that occurred in a widespread web of genetically connected human populations (Multiregional Evolution Model), or (2) a population influx, of a new species, modern *Homo sapiens*, replacing the indigenous archaic populations wherever they lived (Recent Out of Africa Model). Other models, such as the Afro-European *sapiens* Model (Bräuer, 1984, 1989, 1992, 2007), the Assimilation Model (Smith et al., 1989, 2005; Cartmill and Smith, 2009), or the Continuity with Hybridization Model (Wu, 2004), emphasize different balances of gene flow (or migration) between regions and in situ evolutionary change within regions and generally describe hypotheses about human evolution in a particular region of the world.

Models of modern human origins are most appropriately tested at the edges of the Pleistocene human range (i.e., Europe or East Asia) rather than in the center (i.e., Africa) because the hypotheses all make the same claim for how human evolution occurred in Africa where human ancestors originally evolved. That is, *all* current views of modern human origins recognize that in Africa, modern humans evolved from earlier, more archaic populations (and ultimately from earlier ancestors of the genus *Homo*) into modern African populations. However, the models differ *significantly* in their understandings of what happened in other regions of the world, like Europe and East Asia. So, for example, the morphology of the fossil hominid from the Herto Member of the Bouri Formation in the

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Middle Awash in Ethiopia dated to between 160,000 and 154,000 years ago, which is described as “morphologically and chronologically intermediate between archaic African fossils and later anatomically modern Late Pleistocene humans” (White et al., 2003: 742), provides important evidence of the emergence of modern humans in Africa. This is essentially consistent with *all* hypotheses about modern human origins that concur on the evolution of modern humans *in Africa* from more archaic older populations (e.g., Bräuer, 1984, 1989, 1992, 2007; Stringer and Andrews, 1988; Smith et al., 1989, 2005; Cartmill and Smith, 2009; Wolpoff et al., 1984, 2000) but diverge in whether such a transition occurred *only* or uniquely in Africa. In Europe, where the fossil and archaeological record for this transition is relatively rich and generally well dated, this issue has taken the form of addressing the contentious question of whether Neandertals made a significant genetic contribution to modern human ancestry or were a different species from modern *Homo sapiens* that was wiped out by incoming modern humans, from the central and most densely populated portion of the human range, namely Africa. East Asia represents the other extreme geographic edge of human habitation during the Pleistocene, where the earliest firm evidence for humans in China comes from lithics at a number of sites in the Nihewan Basin in North China dating to 1.7–1.36 million years ago (Chen et al., 2010; Bar-Yosef and Wang, 2012), with human fossil evidence somewhat later in time and continuing to the present. But evaluation of the alternative hypotheses about modern human origins has generally followed a different pattern in East Asia than it has in Europe. This chapter will review the current evidence for the origin of modern humans in East Asia, specifically in modern-day China. We do not intend to describe the fossil record for China at length or in detail—there have been a number of English-language reviews (in addition to the extensive Chinese literature) that did this over the past 30 years (Wolpoff et al., 1984; Pope, 1988, 1992a, 1992b; Etler and Li, 1994; Wu and Poirier, 1995; Etler, 1996, 2004). Rather our intent here is to review recently discovered (or recently described or dated) fossils and to reexamine the question of modern human origins in this region in light of those new data, focusing on those fossils that are most relevant to this issue.

From the beginning of paleoanthropological research in China in the first half of the twentieth century when human fossils from the Middle Pleistocene were first discovered in situ at Zhoukoudian, this region has generally been seen by the scholars who described and analyzed fossils as they were excavated as an area in which human populations evolved without a dramatic replacement by modern humans coming from outside the region, such as was often postulated for Europe (Schmalzer, 2008). In 1934, following the death of Davidson Black, the Cenozoic Laboratory of China appointed Franz Weidenreich as honorary director and invited him to study the “Peking Man” fossils from Zhoukoudian. Weidenreich, a German Jewish scientist working on human variation, came to China in 1935 from Chicago, where he had gone the year before (accepting a job offer at the University of Chicago) to escape Nazi persecution. He described and analyzed the material from Zhoukoudian, originally attributed to *Sinanthropus pekinensis*. His work on these fossils set the stage for later interpretations. He argued, from the beginning, for a connection between the skulls from Zhoukoudian and those of modern populations from the region (Weidenreich, 1937a,b), writing “Earlier (1935) I was able to demonstrate that a close connection between *Sinanthropus* and certain groups of the present Mongol race could be assumed” (Weidenreich, 1937b: 317). He based his interpretation initially on the presence of several cranial traits: the *torus mandibularis*, shovel-shaped incisors, Inca bones, and sagittal keeling (Weidenreich, 1937a). In 1943 he argued that even though there were no intermediate forms known between *Sinanthropus* and *Homo sapiens* in China (as there were Neandertal fossils between *Homo erectus* and *Homo sapiens* in the western part of the Old World):

There are clear evidences that *Sinanthropus* is a direct ancestor of *Homo sapiens* with closer relation to certain Mongolian groups than to any other races. Not less than twelve peculiarities, characteristics of the cranial and limb bones of *Sinanthropus* and of the teeth also—some having a high percentage of occurrence in the available specimens—occur with a relatively high degree of frequency in Mongolian groups. (Weidenreich 1943: 276–277)

These twelve characteristics are the presence of a midsagittal crest, parasagittal depression, Inca (extra-sutural) bone, “Mongolian” features of the nasal bridge, “Mongolian” features of the cheek region of the maxilla, “Mongolian” features of the zygomatic bone, maxillary exostosis, ear exostosis, mandibular exostosis, high degree of platymerism of the femur, a strong deltoid tuberosity of the humerus, and shovel-shaped upper lateral incisors. Weidenreich expanded this list to include other features such as presence of a metopic suture, small frontal sinuses, high frequency of third molar agenesis, reduced posterior dentition, profile contour of the nasal saddle and nasal roof (low nasal profile), and rounded infraorbital margins (Weidenreich 1939, 1943).

Since the time that he wrote, Weidenreich’s polycentric model of human evolution has been the dominant, albeit often misrepresented, model of human evolution in China. He wrote:

The peculiarities of the *Sinanthropus* skeleton, to sum up, are neither “adaptive” nor have they any recognizable connection with special functions which could not be performed otherwise. Their transmission to *Homo sapiens* corroborates first the thesis that *Sinanthropus* is a direct ancestor of *Homo sapiens*, and secondly, that there is a closer relationship to Mongols—or at least to certain Mongolian groups—than to any other races, particularly to whites. This statement does not mean that modern Mongols derived exclusively from *Sinanthropus* nor that *Sinanthropus* did not give origin to other races. In any case, it is safe to say that racial groups supplied with those peculiarities have *Sinanthropus* in their ancestry. Had only one character been transmitted, the relationship might be questioned, but as there are *twelve* special features which behave in the same way the coincidence cannot be accidental. (Weidenreich 1943: 253–254)

Weidenreich’s iconic diagram of his polycentric model (Weidenreich 1946: 30; 1947: 201) shows vertical, horizontal, and diagonal lines, which for him represented ancestry, distribution and specialization, and interchange, respectively. The morphological evidence for continuity that he saw convinced him that early Chinese populations made significant genetic contributions to modern populations of the region, but he recognized in addition that those earlier populations were also ancestral to populations in other regions and that ancient populations in other regions also contributed to the ancestry of modern Chinese. In other words, he recognized the importance of gene flow between populations in different regions and he represented it graphically by the diagonal lines in his drawing.

Weidenreich’s polycentric model was famously misappropriated and misrepresented by Coon (1962), who ignored the importance of gene flow and emphasized isolation as the cause of regional differentiation. Howells’ (1942, 1959, 1997) depiction of Weidenreich’s model as a candelabra also perpetuated this misunderstanding. In the views of modern authors who trace their intellectual inspiration back to Weidenreich, this model has been more appropriately likened to a trellis as a metaphor for the evolutionary network of reticulating populations that regularly exchange genes (Wolpoff and Caspari, 1997) or a river that branches, runs for a time as separate streams, but reunites into a single river with water from the separate streams mixing together (Wu, 1999).

Importantly, Weidenreich saw human variation even in the deep past as similar in nature to what we see in the present. He recognized that there were not and never had been “pure races” (Caspari and Wolpoff, 1996) and that the pattern of human variation we see today extended back into the past. He argued that “just as mankind of today represents a morphological and

generic unity in spite of its being divided into manifold races, so has it been during the entire time of evolution” (Weidenreich, 1940: 380). Further, he wrote that “the old theory, claiming that man evolved exclusively from *one* center whence he spread over the Old World each time afresh after having entered a new phase of evolution, no longer tallies with the palaeontological facts” (Weidenreich 1940: 381–382).

Schmalzer’s (2007, 2008) account of the history of human evolutionary studies in China places it in a modern historical, political, and social context. She writes that even after Weidenreich’s work, but before 1952, Chinese scholars “rarely claimed Peking Man as a direct ancestor of modern Chinese people or of modern humans as a whole. By about 1952, however, Peking Man was universally regarded in Chinese science dissemination materials as such an ancestor” (Schmalzer, 2008: 261). By then, the half-million year time gap in the Chinese fossil record between Zhoukoudian *Homo erectus* and the material from Zhoukoudian Upper Cave had been filled in to some extent with new discoveries, so that human evolutionary history was more evenly represented by fossils throughout the chronological sequence (Wu, 1992). Since that time, the fossil record has continued to accumulate, with more fossils having precise geological context and as a result being better dated.

Wu and Zhang (1978) summarized their views that Chinese human evolution was characterized by continuity but *not* by isolation from other populations. They wrote that fossil humans in China “have obvious similarity in physical features, there was definite continuity in the physical development of them,” and “of course, we do not exclude the possibility of exchanging genetic material between China and neighboring regions, but the exchange played less important role” (Wu and Zhang, 1978: 39). Recent Chinese scholars working on the Chinese fossil record have also emphasized in situ evolution (Wu and Wu, 1985; Wu and Dong, 1985; Wu, 1988, 1998, 1999, 2004, 2005, 2006; Chen and Zhang, 1991; Wu and Bräuer, 1993; Wu and Poirier, 1995; Liu et al., 2005; Liu and Wu, 2011, Schmalzer, 2008). For example, Wu and Poirier (1995) pointed to the increase in the fossil record in the late twentieth century and, based on that, identified a number of features that link the material from Zhoukoudian with modern Chinese populations. These include midsagittal elevation, flatness of the nasal saddle, orientation of the antero-lateral surface of the frontal process of the zygomatic, less protruding of the middle face, contour of the lower border of the zygomatic process of the maxilla, lower upper facial index, shovel-shaped incisors, position of the maximum breadth of the skull, roundness of the orbital margins, shape of the sutures between the frontal and nasal and maxillary bones, and lambdoidal ossicle (Wu, 1990; Wu and Poirier, 1995). These features, they maintained, are frequent in Pleistocene specimens from China but rare in specimens outside the region.

In 2004, with an expanded fossil record, Wu (2004) pointed out that although some of these characters are actually primitive to the genus *Homo* rather than strong evidence of a connection between the Zhoukoudian material and modern Asian populations, and these features could be found in fossils from other regions, the morphological constellation seen in China is unique. The cranial features he saw were: fronto-nasal and fronto-maxillary sutures forming a horizontal curve, forward-facing antero-lateral surface of the zygomatic process (making the face flat), curved lower border of the zygomatic process of the maxilla bone, flat nasal region, obtuse zygomaxillary angle (lack of protrusion in the midface), low upper facial height, rounded infero-lateral margin of orbit, presence of a malar tuberosity, and shovel-shaped incisors (Wu, 1992). It is possible that some of these features are part of a functionally integrated system and may not be entirely independent of each other (e.g., the flat face and the flat nasal region may be functionally related), but most of these features are probably independent of one another. We refer to these kinds of morphological features, in this chapter, as “regionally predominant” features. They are not necessarily unique to East Asia, as they occur in other regions as well, but occur more commonly in East Asia. Similarly,

they are not universal in East Asia, simply more common than in other regions. Wu argued that some of the “regionally predominant” features of Pleistocene humans of China that he discussed do not necessarily extend into any of the Holocene materials from East Asia.

But, in addition to evidence for local continuity within the region, some scholars see evidence of contact with other geographical regions. For example, Wu has further pointed to the round orbits on Maba, the weak chignon on many upper Paleolithic specimens from south China (Liujiang, Ziyang, and Lijiang), and the bulging at the basal part of the nasal process of the maxilla (lateral to the upper part of the piriform aperture) of the Dali specimen as features that are reminiscent of morphology seen in European Neandertals and that could be the result of genetic exchange with Europe. Similarly, he saw the flatness of the upper face of Steinheim and various European Upper Paleolithic skulls and the receding glabellar region of Steinheim and Arago as features that could represent genetic exchange in the other direction (to Europe from Asia) (Wu, 1988, 2005). He argued that geographic regions were somewhat but not completely isolated from one another, creating geographic differences between regions. The clearness of the distinction was reduced by even small levels of gene flow. He argued then that ancient China had continuous but not isolated evolutionary change with gene flow from other regions and that the differences between populations living in what is now China and those in other regions were only of different frequencies of morphological features rather than sharply distinctive (Wu, 1988).

In the early years of Chinese paleoanthropology, the fossil record produced what was the largest sample of *Homo erectus* known, but very little evidence of archaic *Homo sapiens*. The evidence for continuity in the more richly known and much better documented East Asian fossil record is even stronger today than it was in Weidenreich’s time. In particular, the chronological gap between the specimens from Zhoukoudian Locality 1 and modern humans has been filled in with temporally intermediate fossil specimens. In addition to evidence for continuity, Wu provided concrete examples of mosaic evolution—morphology that, in part, formed the basis of the pattern in China that was described by Wolpoff et al. (1993), in which no clear-cut demarcation between *Homo sapiens* and *Homo erectus* could be drawn to definitively distinguish these taxa. Wu (1990) argued that many possible features that had been described by other authors as autapomorphies of *Homo erectus* occur in specimens in combination with features that are generally thought to be typical of *Homo sapiens*. These include thick cranial vault bones (the Dali and Xujiayao [Wu and Poirier, 1995] specimens are similar to the *Homo erectus* material from Zhoukoudian), postorbital constriction (present in the Maba skull, but weak in *Homo erectus* specimens from Hexian), frontal sagittal keeling (present in Dali, Jinniushan, and Maba specimens, all considered early *Homo sapiens*), sharply angulated occipital (present in Dali and Jinniushan specimens), prominent angular torus (present on Dali, Ziyang [Woo, 1958; Wu and Poirier, 1995], and Kow Swamp from Australia), and low temporal squama (not present on the Hexian *Homo erectus* cranium). The mosaic co-existence of these putatively autapomorphic features of *Homo erectus* in the same specimens as features typical of archaic *Homo sapiens* is evidence in favor of the evolution of *Homo sapiens* from *Homo erectus* at least in China, supporting a model of continuous evolutionary change in East Asia.

Wu argued that the transition was more usefully seen as change within a chronospecies and that the presence of morphological mosaics between these supposed species is evidence of continuity. In short, Chinese scholars argued that the fact that common features persist throughout the Chinese fossil record and that there is a morphological mosaic between *Homo erectus* and *Homo sapiens* supports the idea of continuity in human evolution in China. In addition and very importantly, Wu (2004, 2005) also emphasized the morphological evidence for gene flow from the western part of the Old World supporting the idea of what he called “Continuity with Hybridization” (Wu, 1998), or Multiregional Evolution. He sees

Multiregional Evolution as a hypothesis for a global-level transition from archaic to modern humans over the last 200,000 years, while his hypothesis of Continuity with Hybridization is meant to apply more narrowly geographically (only dealing with China) but over a longer time span than Multiregional Evolution (namely from the first humans in East Asia to the present). He argues that human evolution in China in the late Middle Pleistocene and Late Pleistocene fits both models, but that Continuity with Hybridization might not apply to other regions of the world.

The view that the East Asian fossil record provides evidence for continuity through time is common among Chinese scholars but is not limited to them. The fullest early articulation of the Multiregional Evolution hypothesis was a chapter by Wolpoff, Wu, and Thorne in the 1984 volume that was the predecessor to this one (Wolpoff et al., 1984). These authors based their model explicitly on Weidenreich's ideas about the evolutionary sequences in different regions of the world and on the idea that "modern populations evolved in different geographic areas from already differentiated ancestral groups of archaic *Homo sapiens* (or *Homo erectus*)" (Wolpoff et al., 1984: 417). They called attention to the East Asian (and Australian) fossil record, which was often overlooked by Euro-centric scholars who focused on the fossil record from their own region. They saw humans as a geographically widespread but interconnected species that originated ultimately in Africa. Colonization outside Africa allowed populations to adapt to local conditions, which led to regional differences. Adaptive changes spread through gene flow to other groups and selective forces that were shared across the geographic range led to similar change. Like Weidenreich's model on which it was based, the Multiregional Evolution Model was often mischaracterized as a model suggesting geographical isolation of human populations in different regions of the world that then evolved independently (Caspari and Wolpoff, 1996; Wolpoff et al., 2000); in fact, the model combines evolutionary change at a global level across the human geographical range and consequent spread of adaptive alleles with continuity of regional morphological features in particular areas. Again, like Weidenreich, Wolpoff et al. (1984) regarded human evolution as a gradual, global process that took place across the entire area of human habitation. Under this model, mosaics of archaic and modern (primitive and derived) traits are to be expected in transitional specimens, and the line between *Homo erectus* and *Homo sapiens* is an arbitrary distinction between chronospecies. In fact, some of these authors took this idea one step further and later argued for sinking the taxon *Homo erectus* into *Homo sapiens* on the grounds that they occupied the same geographic range, had similar regional variation in morphology, and that *Homo erectus* is an earlier chronospecies of *Homo sapiens* with only an arbitrary boundary between one and the other (Wolpoff et al., 1993).

Wolpoff, Wu, and Thorne (1984) saw a number of features that they argued represent evidence of morphological continuity of human fossils in Northeast Asia. These included incisor shoveling ("the most consistent feature characterizing Pleistocene fossil humans in China" [Wolpoff et al., 1984: 434]), facial height reduction, posterior dental reduction, third molar agenesis, flatness of the upper middle face (particularly of the nasal saddle), more orientation of the zygomatic bones that contrast with European specimens and that are more angular in shape when seen in inferior view. They also saw some features whose frequency declined through time but that seemed to occur more commonly in East Asian samples than in other areas, including sagittal keeling, Inca bone frequency (though for extant humans in East Asia, Inca bone frequency is low), size of the frontal sinus, and mandibular exostoses. Finally, a few features occur more commonly in earlier crania, namely the straight-line form of the fronto-nasal and fronto-maxillary sutures and the similarity in size between the upper and middle part of the nasal bones. These features were not unique to Chinese populations even in the Pleistocene but are much less common and disparately represented in other regions. Wolpoff et al. (1984) saw the similarities between archaic and more recent

populations of China in features that are not of obvious adaptive value as clear evidence of continuity of morphology and strong evidence against the possibility of replacement by populations from elsewhere who would not have shared those features. Although, as mentioned above, the multiregional evolution model has often been mischaracterized as a model of independent in situ evolution in different geographic regions (e.g., Chu et al., 1998), the authors explicitly addressed the important issue of gene flow in the final paragraph of their article:

We contend that this is the normal pattern of evolution in *Homo*. It is in situ in the only sense that gradual evolution in a polytypic species can ever be in situ, and it involves gene flow in a manner that evolution in a polytypic species always must. The origins of modern *Homo sapiens* are to be found in the evolutionary process we have described as multiregional evolution, and not in Noah's Ark. (Wolpoff et al., 1984: 471)

Hence, multiregional evolution did not suggest independent origins of modern humans in places like East Asia (Wolpoff et al., 2000), rather it recognized Africa as the center (and source) of human populations prior to modern human origins, with smaller populations spread over the rest of the Old World.

Wu (1999) saw human evolution in China not as a ladder or bush (which has branches that separate but never come back together as a single branch) but as a river network, in which there is continuous evolution (i.e., the main stream) but branching of smaller streams (local populations) that may disappear (become extinct), may join with other branches coming from other regions, or may join back to the main stream. This is a metaphor for what Wolpoff and Caspari have referred to as reticulation (Wolpoff and Caspari, 1997).

Following the discoveries of several important human fossils by the late 1980s (including Qu Yuan River Mouth, Jinniushan, Dali, Jianshi, Dadong, Nanjing), there were new examinations of the Chinese evidence. Reviews of the Chinese fossil record written by western scientists have also generally, but not always, taken the view that the fossils provide strong evidence for continuity. In evaluating the Chinese human fossil record in the late 1980s, Pope (1988: 62) wrote that "in the Far East, a model favoring the local evolution of *Homo sapiens* from *Homo erectus* rather than a replacement model is indisputably the most parsimonious interpretation of the current evidence." His analysis of the craniofacial evidence for modern human origins in China demonstrated for him that the fossil record could not be explained by any kind of replacement model of modern human origins (Pope, 1992a). He argued instead for the Assimilation Model, which he described as a variant of the regional Continuity Model. In addition, he argued that the archaeological record "is an especially large impediment to the acceptance of complete replacement of indigenous populations by invaders possessing a superior technology (contra Klein, 1992). There is no evidence for the introduction of major technological innovations" (Pope, 1992a: 291, 1992b). At the time he wrote, the genetic evidence could not be reconciled with this interpretation of the fossil and archaeological record, a point that Pope acknowledged needed resolving (Pope, 1988).

Similarly, Etler (1996) argued that the newly discovered material clearly demonstrates "morphological continuity between archaic and modern human beings in China. This continuity, moreover, is not solely contingent on the persistence of discrete regional traits through time but rests on the documentation of a series of mosaic transformations that show a steady temporal progression, i.e. a process of sapienization from *H. erectus* to premodern *H. sapiens* and across the phylogenetic Rubicon to early modern human beings in Asia" (Etler, 1996: 293). Brown (1992, 1999) argued that there was strong evidence of continuity between late Pleistocene and mid-to-late Holocene people living in China but found it difficult to extend that back into the Middle Pleistocene because of limited fossil specimens and poor chronometric dates.

In summary, three types of arguments for continuity of human evolution in China have been made. First, scholars have argued for regional morphological features in the human fossil record and modern humans that link specimens from China. Weidenreich listed twelve of these features that he saw as support for a connection between the material from Zhoukoudian Locality 1 and modern populations of China. Although some of these regionally predominant features have been shown to be primitive to *Homo* and not unique to China, the morphological complex of some features does characterize specimens from China (Wu, 2004). Second, the transition between *Homo erectus* and archaic *Homo sapiens* in China has been shown to be characterized by a morphological mosaic rather than a clear-cut demarcation or an abrupt transition (Wu, 1999). The degree of postorbital constriction of the Maba and Hexian specimens and the debates about the taxonomic assignment of specimens like Jinniushan and Dali reflect this mosaic, which is what we would expect from a gradual transition between chronospecies rather than a replacement of one species by another. Finally, the archaeological record shows that there is no interruption of the Chinese Paleolithic sequence that would correspond to an influx of populations from elsewhere.

As mentioned above, although Chinese scholars generally see evidence of continuity in the Chinese fossil record, and although many western scholars have reached the same conclusions, there are others (virtually all western scholars) who do not regard evidence from this region of the world as support for continuity. Stringer and Andrews (1988) argued that late Middle to Late Pleistocene Chinese fossils were actually more similar to other Middle Pleistocene hominids from further west and different from early hominids from the region. They questioned the nature of the transitional features that had been noted by advocates of the Multiregional Model and suggested that more detailed work was needed before such conclusions could be drawn. Lahr (1994) criticized the morphological basis of the Multiregional Model in a quantitative examination of the individual traits that had been proposed to provide evidence for evolutionary continuity between Chinese *Homo erectus* and modern Chinese populations. She suggested that multiregional evolution predicts that as a reflection of morphological (and evolutionary) continuity, certain sets of cranial features will occur either exclusively or at least with higher frequency in particular regions. She interpreted her results to constitute a strong rejection of multiregional continuity, as she found that regional features that were claimed by the Multiregional Model to characterize the East Asian human fossil record were found in other regions, in some cases in higher frequencies. Wolpoff (1999) argued that given the higher population size of Pleistocene Africa than other parts of the world, one should expect more modern genes (and morphology) to have African rather than East Asian origins. He argued that her work fails to refute Multiregional Evolution and is in fact compatible with its expectations (Wolpoff, 1999: 780). Lieberman (1995: 173) criticized the suggestion (going back to Weidenreich 1943) that the high frequency of the malar notch in Pleistocene China is evidence of continuity, writing “an incisura malaris, however, is absent on many modern Chinese skulls such as those from Upper Cave 101(Zhoukoudian).” As with Lahr’s critique, however, Lieberman’s argument fails to consider that features may be more common to a particular region, that is, regionally predominant, without being either ubiquitous in that region or unique to that region. In fact, the occurrence of gene flow, essential to the Multiregional Model, would predict exactly this pattern. Similarly, a quadrangular shape of the orbit has been claimed to be a common feature among Pleistocene humans in China indicating continuity in the region, but Lahr (1994) has written that the orbits of modern Chinese are very variable in shape. Note the importance of distinguishing between modern (i.e., recent or living) populations and Pleistocene populations. Modern Holocene Chinese may not show the same evidence of continuity with Pleistocene material as early moderns in China due to higher levels of gene flow resulting from population expansions and movements in recent times.

Testing hypotheses about modern human origins in the region requires comparing archaic specimens from China with succeeding early modern humans from the same region, in addition to later populations. Finally, in addressing the question of modern human origins in this region, Bae (2010) reviewed the late Middle Pleistocene hominid fossil record in Eastern Asia and noted a number of problems connected to dating and taxonomic assignment of fossils that suggest to him that there is a great need for an improvement in both the quantity and the quality of the Asian human fossil record, preferably in the context of large-scale multidisciplinary projects that would provide excellent geological and archaeological context.

Until recently, evidence from human mitochondrial DNA showing low genetic variation was often interpreted (Cann et al., 1987; Stringer and Andrews, 1988) as evidence of a population bottleneck. This was taken as support for a model of complete replacement of archaic humans in all non-African regions of the world by modern humans who evolved in Africa. Important dissenting voices (e.g., Templeton, 1993, 1997, 2002; Relethford, 2001; Hawks and Wolpoff, 2003) suggested other interpretations of the low genetic diversity seen in living humans. Recent sequencing of Neandertal (Green et al., 2010) and Denisovan (Reich et al., 2010) nuclear genetic material has shown the persistence of genes from those ancient specimens in modern human populations, making it clear that the relationship between Neandertals and archaic humans elsewhere in the Old World on the one hand and later populations on the other was much more complex than a simple replacement model would suggest. This leads to questions about how we should expect the morphology evident in the human fossil record to look under a hypothesis of more genetic exchange between ancient populations than some had previously supported.

Recently Discovered or Described Human Fossils from East Asia

In this chapter, we focus on human fossils from East Asia that have been discovered or described in the last 25 years or so (since the previous edition of this book [Smith and Spencer, 1984] was published). The reviews cited above summarized and synthesized the state of knowledge of human evolution with respect to models of modern human origins at the time they were written. We will update those in light of recent discoveries in terms of human fossils, dating, archaeology, and analysis of ancient DNA.

Table 3.1 lists relevant human fossil material¹ from China; the geographic position of material discussed here is shown on the map in Figure 3.1. We have listed English-language citations for each fossil site. The important fossil material that was discovered earlier than the 1980s has been ably reviewed by a number of authors (Wolpoff et al., 1984; Wu and Poirier, 1985; Pope, 1988, 1992a, 1992b; Etler, 1996). Here we focus on more recently excavated material to reexamine these hypotheses in light of an expanded fossil record, discussed in the context of our best understanding of their chronological age.

So, what is different today than was the case in 1984 when the previous edition of this book was written? The human fossil record from East Asia, in particular from China, has grown significantly since 1984, and many of these fossils were discovered *in situ* and as a result are much better dated radiometrically or by associated fauna than those that were discovered earlier. The importance of reliable chronometric dates is critical to testing hypotheses about modern human origins, as it provides a temporal context to events that happen through evolutionary time. Finally, the evidence from ancient DNA, in particular from the Denisova specimen in Siberia, has allowed us to test models about modern human origins using genetic data in addition to the fossils that constitute direct evidence of human evolutionary change.

Table 3.1 Human fossils from East Asia.

Site	Fossils	Age in Thousand Years	Reference
Yuanmou	Upper incisors	1700 (paleomag)	Zhu et al., 2008
Guojiabao	Left tibia	1000 minimum	Wu and Poirier, 1995
Gongwangling, Lantian	Partial skull	750–1150 (paleomag)	Wu and Poirier, 1995
Chenjiawo, Lantian	Mandible	650–500 (paleomag)	Wu and Poirier, 1995
Yunxian (Quyuan River Mouth)	Two crania	581 ± 93 (ESR) 870–830 (paleomag)	Chen et al., 1997
Zhoukoudian (Locality 1)	Six skullcaps, other dental, gnathic and postcranial material	230–578 (ESR amino acid racemization, fission track, thermoluminescence, and uranium series)	Huang et al., 1991 Wu and Poirier, 1995
Hexian	Skullcap, cranial fragments, mandible, isolated teeth	150–270 (uranium series)	Liu and Wu, 2011
Jinniushan	Complete skull and much of skeleton	260 (ESR, uranium series)	Chen et al., 1994
Chaoxian	Occipital	160–200 (uranium series)	Liu and Wu, 2011
Dali	Complete skull	281 (ESR/uranium series)	Yin et al., 2011
Changyang	Partial maxilla	170–220 (uranium series)	Wu and Poirier, 1995
Dingcun	Parietal, teeth	160–210 (uranium series)	Wu and Poirier, 1995
Tongzi	Teeth	113–181 (uranium series)	Liu and Wu, 2011
Zhoukoudian (locality 4)	Premolar	171–124 (uranium series)	Wu and Poirier, 1995
Maba	Skullcap	135–129 (uranium series)	Liu and Wu, 2011
Dadong	Four teeth	130–300 (uranium series, fauna, ESR)	Liu et al., 2013
Xujiayao	Cranial bones of ten individuals	125–204 (uranium series)	Liu and Wu, 2011
Zhirendong	Mandible, two molars	> 100 (uranium series)	Liu, Jin, et al., 2010
Huanglong Cave	Seven teeth	103–44 (uranium series and ESR)	Liu, Wu, et al., 2010
Liujiang	Complete skull and associated postcrania	Late Pleistocene	Wu, 1992
Tianyuan Cave	Mandible, associated postcrania	42–39 (AMS radiocarbon)	Shang et al., 2007
Chuangdong	Two skulls	Late Pleistocene	Wu and Poirier, 1995
Jianping	One humerus	Late Pleistocene	Wu and Poirier, 1995
Lijiang	One cranium	Late Pleistocene	Wu and Poirier, 1995
Miaohoushan	Two parietal fragments and one radius	28 (radiocarbon)	Wu and Poirier, 1995
Jingchuan	Cranium without facial or basilar portion	48–15 (OSL)	Wu and Poirier, 1995
Shiyu	Occipital fragment	28.9 (radiocarbon)	Wu and Poirier, 1995
Salawusu	Cranial bones, limb bones	50–37 (uranium series)	Wu, 1992
Wushan (Yuanyuang)	Skullcap, other cranial bones	38.4 (radiocarbon)	Wu and Poirier, 1995
Laibin	Cranial base	Late Pleistocene	Wu and Poirier, 1995
Minatogawa	5–9 skeletons	18 (radiocarbon)	Suzuki and Hanihara, 1982
Ziyang	Incomplete skull	39–37 (radiocarbon)	Woo, 1958; Wu and Poirier, 1995

Table 3.1 (Continued)

Site	Fossils	Age in Thousand Years	Reference
Salkhit	Skullcap	Probably late Pleistocene	Coppens et al., 2008
Maludong	Range of cranial and postcranial remains	13.6–14.3 (cal yr. radiocarbon)	Curnoe et al., 2012
Longlin Cave	Partial cranium	11.5 K \pm 255 (cal. yr radiocarbon)	Curnoe et al., 2012
Upper Cave Zhoukoudian	Three complete skulls and associated material	34–29 (radiocarbon)	Chen et al., 1992; Wu and Poirier, 1995

**Figure 3.1.** Map of East Asia showing the position of sites of important human fossil discoveries made or described since 1984 and discussed here.***Yunxian (Quyuan River Mouth)***

Two fossil human crania were discovered in terrace deposits of the Han River in Hubei Province in 1989 and 1990 (Li and Wang, 2001). ESR dating (early uptake model) on associated animal teeth produced a date of 581 ± 93 ka (Chen et al., 1997), a date that is at odds with the geomagnetic dating of 830–870 ka. Although the crania are quite crushed and deformed,

Li and Etler (1992) reported that they are complete adult male specimens with a mixture of features associated with *Homo erectus* and archaic *Homo sapiens*. Li et al. (1991) estimated the cranial capacities at about 1,100 cc. Li and Etler (1992) and Etler and Li (1994) argued that although they show derived facial morphology and large cranial dimensions, they also exhibit more broadly archaic (*Homo erectus*-like) features, such as the morphology of the tympanic, temporal squama, frontal squama, supraorbital torus, and poorly flexed cranial base. They concluded that the crania are “demonstrably more primitive than Chinese hominids from Dali and Yingkou (Jinniushan)” (Li and Etler, 1992: 407), convincing them to place the specimens in *Homo erectus*. Wu and Poirier (1995) pointed to the postorbital constriction and low position of the maximum breadth of the brain case as *Homo erectus*-like features, but they recognized other features that link the crania to archaic *Homo sapiens*. Zhang (1995) argued that because of damage and distortion, some features are of doubtful use in determining whether these specimens belong to *Homo erectus* or *Homo sapiens*. He suggested that based on undistorted features, the specimens seem more similar morphologically to early *Homo sapiens*. Li and Etler (1992: 407) made the important point that a comparison of these fossils to other Middle Pleistocene fossils from East Asia shows considerable variation and “differential distribution of character states associated with *H. sapiens* in regionally disparate Middle Pleistocene human populations,” suggesting that the emergence of modern humans was not an event that took place in one region of the world. Rather, they concluded that “it is best to view all Middle Pleistocene hominids in a broad perspective as an essential part of one evolving lineage in direct ancestry to modern humans” (Li and Etler 1992: 407).

Nanjing

Two partial human crania and a human upper second molar were discovered in 1993 in Hulu Cave near Tangshan, east of Nanjing in Jiangsu Province. Skull 1 (Figure 3.2; Wu et al., 2002) was originally thought to be 350 ka according to ESR and U-series dating (Chen et al., 1996). The flowstone cover above the skull was more recently dated to more than 500 K with a maximum date of 620 ka (Liu et al., 2005), but this layer is not sealed, so that the skull below the layer is not necessarily earlier than the calcium layer above it. In fact, the upper molar found together with the skull below the covering layer is much more similar to that of modern humans than to *Homo erectus*, according to both metric and nonmetric characters (Zhou, 2002). Furthermore, Zhao et al. (2001) have obtained a date of 130 ka for an animal tooth buried under this calcium covering layer. According to the mammalian fauna and paleoclimate data, Skull 2 may be dated between 183 and 127 ka (Xu, 2002). In short, Skull 1 is much older than Skull 2 and may be similar in age to the *Homo erectus* material from Zhoukoudian (Liu et al., 2005). An analysis of the morphology of the Nanjing 1 cranium indicates that it shares many features of *Homo erectus* with other members of that species from Africa and Europe (including a low, flat frontal bone, postorbital constriction, occipital torus, and angular torus in the parietal bone). In addition, it shares cranial features with *Homo erectus* from Zhoukoudian (including cranial shape, though it is smaller overall than most of the Zhoukoudian skulls) but also exhibits what the describers consider to be regional differences (within East Asia) from the more northern Chinese sample (such as small overall size, with a cranial capacity of only 860 cc, projecting nasal bone; Liu et al., 2005; Zhang and Liu, 2005), suggesting the presence of a morphological gradient across space in Eastern Asia in the Pleistocene (Wolpoff, 1999: 499), which has been suggested to represent climatic adaptation (Zhang and Zhang, 2004; Zhang, 2006, 2009; Zhang and Liu, 2010). The obvious protruding nose is quite different from that of most other human fossils from China and is reminiscent of morphology more commonly seen in Europe and Africa (Wu and Shang, 2007); this may be evidence of gene flow from those regions. The second Nanjing cranium is more robust,

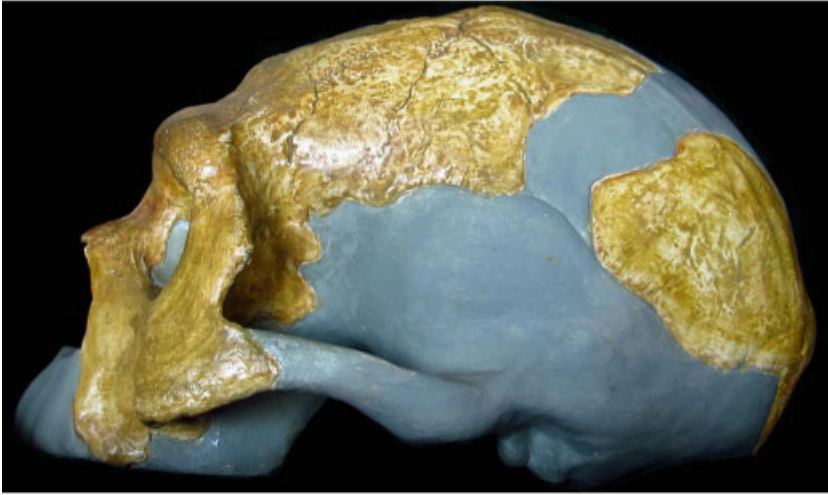


Figure 3.2. Lateral view of Nanjing 1 cranium.

with thicker cranial bone, a moderately expressed midline keel, bregmatic eminence, and well-developed nuchal torus (Wolpoff, 1999). The midline keel is broad-based and very low—this morphology is very different from that of *Homo erectus* in China and is generally more similar to what is seen in the Petralona and Kabwe specimens (Shang and Wu, 2002), again consistent with gene flow from the west.

Jinniushan

The Jinniushan specimen was discovered in 1984 near Yinkou in Liaoning Province in Northeastern China in an isolated karst prominence in a fissure of a collapsed limestone cave. It was excavated in 1984 by a team directed by Lü Zuné. It is very unusual in the Chinese fossil record from this time period in that it includes many skeletal elements from a single individual (Lü, 2003). The human skeleton was discovered near the base of 15 meters of deposit in the bottom of layer 7, which also contained the remains of Pleistocene fauna. ESR and uranium-series dating of animal teeth from that layer suggest a date of about 260,000 BP, consistent with the faunal assemblage (Chen et al., 1994). Later dates that were previously reported for this site were from higher stratigraphic levels than the human remains. The skeletal remains derive from a single adult individual, represented by a cranium, with most of the maxillary dentition, six vertebrae (one cervical and five thoracic), two left ribs, a complete left patella, a complete left ulna, complete left os coxae, and numerous bones of both hands and feet. Although initial reports suggested that this individual was male (Lü, 1990, 1994), the morphology of the pelvis and a comparison of the skull with the penecontemporaneous specimen from Dali suggest that it is likely female (Lü, 2003; Rosenberg, et al., 2006). Like Dali and Maba, the specimen exhibits a mosaic set of features, making it an excellent transitional form. The cranium (Figure 3.3) has very thin vault bones, a gabled cranial contour, a broad frontal bone, central supraorbital thinning, and marked nuchal plane reduction—a constellation of features that has been argued as evidence for early modernity in an Asian specimen (Wolpoff, 1999: 576). The specimen also has archaic features, including broad interorbital distance, projecting supraorbitals, and broad nuchal torus. Finally, it has some features that are distinctly reminiscent of earlier individuals from China



Figure 3.3. Three-quarter view of the Jinniushan cranium.

(such as Zhoukoudian and Yunxian), including arched supraorbitals, that are separated from the frontal squama by a sulcus, a keel on the frontal bone, a wide but vertically oriented face, horizontal naso-frontal suture, incisor shoveling and M^3 reduction (Wolpoff, 1999: 577). Estimates of cranial capacity average $1,330\text{ cm}^3$ and estimates of body weight based on a number of different measures average 78.6 kg, making this specimen the largest female known in the human fossil record from anywhere in the world (Rosenberg et al., 2006). The individual has a very robust pedal skeleton (Lü et al., 2011). Because many elements from a single individual are present, it is possible to examine intraindividual metrics. The individual has body proportions typical of cold-adapted populations elsewhere in the world and an encephalization quotient of 4.15, similar to estimates for late Middle Pleistocene humans based on unassociated specimens and suggestive of similar patterns of encephalization in far Eastern Asia that we see elsewhere in the Old World (Rosenberg et al., 2006).

Dali

The Dali specimen (Figure 3.4) is penecontemporaneous with the Jinniushan specimen. It was discovered in 1978 in river gravels of the ancient Luo River, near Jiefang Village, Dali County, Shaanxi, in association with small stone flake tools and Palearctic fauna (Bae, 2010) and has been studied by Wu Xinzhi. Chen et al. (1984) reported a uranium series date for Dali of $209 \pm 23\text{ ka}$, but Pope (1992a) argued that the faunal evidence, the paleosols, and other evidence suggest that the specimen may be older, perhaps as old as 300 ka. ISR/ESR studies put the fossil between 300 and 260 ka (Yin et al., 2002). A new date of ESR/U-series is $281 +46/-41\text{ ka}$ (Yin et al., 2011). It is a robust male skull that Wu and Wu (1985) estimated was under 30 years old at the time of death. The braincase is long, low, and wide with a cranial capacity of 1,120 cc. The cranial bones are extremely thick, especially in contrast to Jinniushan. The supraorbital torus is robust, arching over the orbits with a separation at glabella. It is thickest near the midline, as is also the case in the Petralona, Bodo, and Kabwe specimens. The temporal lines and the supramastoid ridges are well developed (Wu and



Figure 3.4. Anterior view of Dali cranium.

Poirier, 1995). Most cranial metrics put the Dali specimen within the range of variation of western archaic *H. sapiens* and intermediate between *H. erectus* and late *H. sapiens* (Wu and Poirier, 1995). In some features [such as a shape ratio of the occipital bone expressed as (height/breadth) \times 100], Dali (at 104.3) falls in the modern range of variation (101.6–124.5) and differs from Middle Pleistocene Europeans (82.0–99.2). Non-metric features of the skull also place it more like early *H. sapiens* than *H. erectus*, but it also has many features typical of *H. erectus*. The configuration of the glenoid region is intermediate between *Homo erectus* and modern humans (Pope, 1992a). The face is fairly broad, flat transversely, and is similar to the faces in the Jinniushan and Nanjing specimens. Other regionally predominant East Asian features include the presence of a maxillary notch, an elevated lower cheek border, large angle of nasal bones to the face, forward-facing orbital pillars, narrow, flat nasal bones, constricted internasal crest, horizontal naso-frontal suture, and swelling of the maxilla (Wolpoff, 1999: 576). There is a bulge on the anterior surface of the lower part of the nasal process of the maxilla (between the medio-inferior corner of the orbit and the upper section of the lateral border of piriform aperture), similar to the morphology seen in Petralona, Kabwe, and Bodo and different from all other Pleistocene human skulls known from China (Wu, 1988). The infero-lateral border of the orbit is blunt. Brown (2001) argued that the vault was robust with a mosaic of features typical of both *H. erectus* and *H. sapiens*, and Wu (2009), who described the Dali cranium, contends that the face is much more like modern *H. sapiens*. He argued that its morphology indicates that the Dali specimen represents one of the members of a continuous lineage in China, with some morphological evidence that indicates probable gene flow from the western part of the Old World (Wu and Athreya, 2013).

Both Dali and Jinniushan preserve important facial skeletons, which is unusual in Chinese Middle Pleistocene species. Both can be seen as transitional specimens, like the Narmada specimen from India that Athreya (2010) has argued cannot be comfortably placed in a *Homo erectus* taxon, “contradict[ing] scenarios that propose a dead-end Middle Pleistocene hominin lineage in Asia, replaced by an advanced *H. sapiens* dispersal from elsewhere” (p. 139).

Chaoxian

This specimen includes a maxillary fragment with both lateral incisors and right P³-M¹ as well as isolated left P⁴-M² and an occipital bone, dated to 200–160 kya BP. The occipital has a suprainiac fossa, which is otherwise not found in human fossils from East Asia but is common in Neandertals (Liu and Wu, 2011).

Dadong

In the early 1990s, excavations at Dadong Cave in Guizhou Province discovered many mammalian faunal remains, stone tools, evidence of fire, and four hominid teeth (I¹, C_x, P³, P₃). The fauna suggests that the deposits span the time from the early Middle to Upper Pleistocene. The incisor specimen, which was discovered during screening of brecciated sediments, is part of the lingual surface of an adult central maxillary incisor that exhibits considerable wear. The tooth shows some evidence of shoveling, with a large lingual tubercle and finger-like projections (Huang et al., 1995; Liu et al., 2013). The other teeth were discovered in situ. The lower canine has a cingulum on the labial side that extends to neighboring sides. The shape of the root is closer to that of *Homo erectus* than to *Homo sapiens* in that it tapers gradually to the apex along the entire length rather than becoming abruptly narrow. The canine and incisor exhibit more archaic features than the premolars, presenting a mosaic of primitive and derived traits (Liu et al., 2013) and showing similarities to Middle and Upper Pleistocene fossils from East and West Asia and Europe (but not especially to Neandertals). Liu et al. (2013) suggest that this mosaic of primitive and derived features is evidence of high morphological diversity of East Asian populations from this time period. This early occurrence of modern traits suggests that modern humans may have appeared earlier in East Asia than previously thought (Liu et al., 2013).

Zhirendong

The recently reported Zhirendong material (Figure 3.5) from south China was discovered in 2007 and is securely dated to the initial Late Pleistocene (> 100,000 years ago) by U-series dating on the overlying flowstones and consistent late Pleistocene faunal assemblage, placing it in MIS 5 or possible MIS 6. (Liu, Jin, et al., 2010). The material includes an anterior mandibular corpus (Zhiren 3) and two isolated molars (Zhiren 1 and 2) excavated in situ. The worn teeth have small crowns that appear to be similar to early modern humans from the Late Pleistocene in Western Asia and Europe. The describers of the material argue that the mandible “represents the oldest evidence of derived modern human morphology in East Asia” (Liu, Jin, et al., 2010: 19204), possessing some aspects of morphology that align it with other early modern humans, but with other features that “distinguish it from most (but not all) Late Pleistocene early modern humans.” They argue that the presence of derived features of mandibular morphology (“distinctly projecting tuber symphyseos, associated mental fossae and modest lateral tubercles” quite different from archaic humans) in the context of a very robust mandibular corpus whose cross-section is in the range of Late Pleistocene archaic samples, above the Middle Pleistocene range but below the earlier Upper Paleolithic modern humans, represents a complex mosaic that reflects *both* “populational continuity (to whatever degree) and admixture in East Asia.” This specimen fits into the “large temporal gap between the latest archaic and earlier modern forms in East Asia” pointed to by Smith et al. (1989: 52) and Bräuer (1992). The fact that this modern morphology appears in China so far in time before the emergence of Upper Paleolithic archaeological assemblages suggested to the authors that morphological and behavioral modernity (in the form of upper Paleolithic tools) were not coincident in this part of the world, further

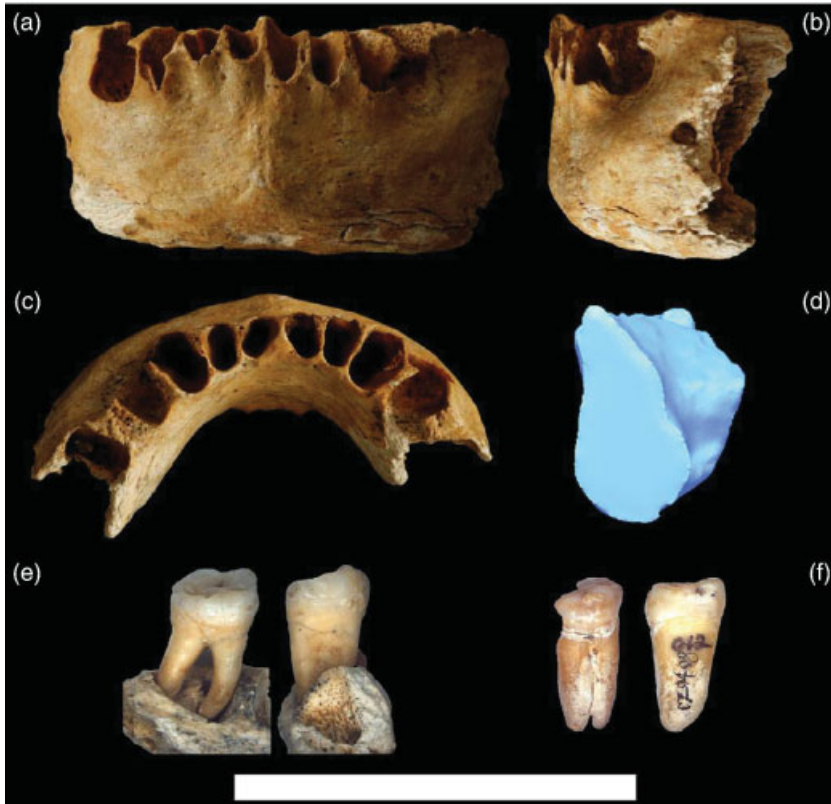


Figure 3.5. The human remains from Zhiren Cave. The Zhiren 3 mandible in anterior (a), lateral left (b), and superior (c) views. The midsymphyseal cross-section of the Zhiren 3 mandible (d). The Zhiren 1 M3 in buccal and mesial views (e), and the Zhiren 2 M3 in the same views (f). (Scale bar, 5 cm.) Photograph reprinted courtesy of Professor Liu Wu, Institute of Vertebrate Paleontology and Paleoanthropology.

evidence against a simple single replacement scenario. The mosaic nature of the mandible suggests that dispersal of modern populations involved gene flow with indigenous populations of East Asia. While the authors recognize that the fossil data do not allow us to estimate the levels of gene flow, they conclude that the morphological mosaic present in this specimen is inconsistent with any “out-of-Africa” population replacement model of modern human origins in East Asia. The Zhirendong mandible is *direct* evidence that the transition from archaic to modern humans that is evidenced in Africa by material like that from Klasies River Mouth also took place at the other edge of the range of human habitation in China. Recently described material from Tam Pa Ling in Laos provides evidence of anatomically modern human cranial and dental morphology from Southeast Asia from a secure stratigraphic context dated to about 50 ka cal BP (Demeter et al., 2012).

Tianyuan Cave

In a cave site very near Zhoukoudian, southwest of Beijing, a human skeleton comprised of thirty-four skeletal elements was excavated and dated by direct accelerator mass spectrometry radiocarbon dating to 42,000–39,000 years before present (Shang et al., 2007; Shang and Trinkaus, 2010). The elements of the skeleton (see Figure 3.6), which may have



Figure 3.6. The human remains from Tianyuan Cave. Photograph reprinted courtesy of Professor Liu Wu, Institute of Vertebrate Paleontology and Paleoanthropology.

been a burial, include a portion of mandible, two isolated teeth, the axis, two parts of the sternum, both scapulae, both humeri, a radius and an ulna, three carpals, five hand phalanges, both femora and tibiae, the distal portion of a fibula, a talus, a calcaneus, four metatarsals, and two foot phalanges. The describers of the specimen argue it has many modern human features, especially on the mandible (in terms of the distinct mental eminence and a number of other features) but also including the modest robusticity on the arms and hands, the presence of a ventral sulcus on the scapula, the presence of pilasters on the femora, the longitudinal sulci on the tibia and fibula, and long talar neck. The skeleton also has a few archaic human features in the upper limb (such as a long proximodistal length of the hamulus, which is Neandertal-like) and interestingly, a moderately high crural index, a reflection of its large lower limb articular surface relative to stature. In these respects it is Neandertal-like and similar to the Jinniushan specimen, indicating an “individual with a markedly stocky body, one normally associated with colder climates and hence higher latitudes” (Shang and Trinkaus, 2010: 192). In terms of the ratio of anterior to posterior dental dimensions, the Tianyuan specimen falls close to the Neandertal mean but between late archaic humans and Upper Paleolithic early modern *Homo sapiens*. Those proportions are quite distinct from Middle Paleolithic modern humans (Shang et al., 2007: 6576). Finally, there are other features for which the Tianyuan 1 specimens falls within the area of overlap between late archaic and early modern humans. Shang and Trinkaus (2010: 195) suggest that the presence of this suite or mosaic of features in Tianyuan 1 at about 40,000 BP is evidence both that there was substantial gene flow of “recognizable modern humans eastward across Eurasia” rather than the independent evolution of these traits in different regions and that a complete replacement event of modern humans from outside the region was unlikely.

Liujiang

Although the Liujiang specimen from Guangxi Zhuang Autonomous Region was excavated in 1958 and described soon after (Woo, 1959), it has more recently been dated with U-series dating to at least ~68 ka, or ~111–139 ka, or perhaps to older than ~159 ka (Shen et al., 2002). The fact that the precise stratigraphic provenience of the specimen within the sites is unknown means that the dates are completely uncertain because we cannot associate the fossil with any of the dates that are known from the site. Liu et al. (2006) argue that the very close similarity of the Liujiang specimen with modern Chinese and the uncertainty in the provenience of the fossils makes it unlikely that they are as old as 67 ka. The fossil includes a fairly complete skull, with most of the maxillary dentition, four thoracic and five lumbar vertebrae, a sacrum, rib fragments, an innominate bone, and two femoral shaft fragments (Wu and Poirier, 1995). The material is clearly modern in morphology though it retains a few archaic features such as the morphology of the lower orbital margin (Liu et al., 2006). According to Liu et al. (2006) the shape of the Liujiang orbit is low, flat quadrangular, while the orbits of modern Chinese are generally higher and closer to circular or elliptical. It appears, then, that the low orbit is the primitive condition among fossil humans in China, while in Pleistocene humans from China, the infero-lateral margin of the orbit is blunt. The one exception to this generalization is the Maba specimen, in which the margin is sharp. This may be the result of gene flow from populations like Neandertals to the west. The occipital bun (or chignon) of the Liujiang specimen may be evidence of gene flow from Neandertals. Lieberman (1995: 168) argued that occipital bunning is probably the result of “more rapid posterior growth of the cerebral hemispheres relative to the formation of the cranial vault bones,” as suggested by Trinkaus and LeMay (1982: 33). He suggested that the occipital bun is a “convergent, epigenetic trait in large-brained dolichocephalic individuals and not

homologous between Neandertals and some early modern humans,” providing support in his view for the Recent African Origin hypothesis of modern human origins, which would predict a narrow cranial base in Europeans, Australians, and Africans. But the Chinese fossil record is inconsistent with this statement. Liujiang, Ziyang, Lijiang, and Chuandong all have occipital bunning, with cranial indices of 75.1, 77.4, 76.8, and 77.9, respectively, while all the Late Pleistocene skulls from Upper Cave (which have cranial indices of 70.1 for UC 101, 69.4 for UC 102, 71.2 for UC 103, making them dolichocranic or even hyperdolichocranic) lack an occipital bun (Wu and Poirier, 1995). Finally, the Liujiang specimen is unusual in having preserved postcranial remains that exhibit suggestions of modern Chinese regional features of the pelvis, particularly in the region of the greater sciatic notch (Wu, 1997; Rosenberg, 2002).

Laishui

A largely complete fossil human skeleton from the Late Pleistocene was discovered in Hebei Province in 1988 and excavated by Professor Lü Zuné. It has not yet been fully described. It is reported as dating either to 28 ka (Etler, 1996) or to between 60 and 30 ka (Etler, 2004; Norton and Jin, 2009) and seems to possess a mosaic of archaic and modern traits, including robust supraorbital tori, “a sloping forehead, along with a robust but essentially modern cranial vault, cranial base and face” (Etler 2004: 45). A protruding nose is reminiscent of populations to the west.

Longlin Cave and Maludong

Most recently, Curnoe et al. (2012) published a description of material from two later Pleistocene sites in southwest China that were discovered in 1979 and 1989, respectively. Longlin Cave is in Guangxi Zhuang Autonomous Region and produced material that includes a partial human cranium, partial mandible (with both mandibular and maxillary dentition), and some fragments of postcrania. Maludong (Malu Cave, or Red Deer Cave) is located in Mengzi County, Yunnan Province. The human material from this site includes a number of cranial fragments as well as a hemimandible and portions of many postcranial elements. The Longlin Cave material was dated to $11,510 \pm 255$ calyr. BP (Curnoe et al., 2012), while the Maludong material comes from deposits dating from $14,310 \pm 340$ calyr. to $13,590 \pm 160$ calyr. (Curnoe et al., 2012). The describers argue that this material seems to belong to a single population that presents an unusual combination of modern and archaic characters unlike any Pleistocene or recent populations of *H. sapiens* (p. 20). The authors interpret their multivariate analysis of the vault shape of LL 1 and MLDG 1704 “to show a unique cranial shape among all later Pleistocene humans” (Curnoe et al., 2012: 21). They suggest two possible plausible explanations for the unusual mosaic of morphology seen in these specimens: that they are evidence of a late-surviving archaic population or that they are evidence that East Asia “may have been colonized during multiple waves during the Pleistocene, with the Longlin-Maludong morphology possibly reflecting deep population substructure in Africa prior to modern humans dispersing into Eurasia” (Curnoe et al., 2012: 1). Although the authors stop short of saying in print that this population could represent a species other than *Homo sapiens*, the popular science press reported that as a possibility (see, e.g., Bower, 2012). In fact, it seems more likely that the fossils represent East Asian modern *H. sapiens* similar to penecontemporaneous fossils like the Upper Cave material from Zhoukoudian. Some of the features mentioned by the authors represent East Asian features (flared zygomatic bones), others are archaic (thick cranial bone), while others

(such as the brain size) actually fall within the modern range rather than representing archaic features, as they suggest. The material does have a mosaic of features but it seems to fit into the normal range of variation in modern humans. There is thus no evidence that it is distinctive enough to warrant the assignment of a separate species.

Huanglong Cave

Seven human teeth from a number of individuals were discovered in Huanglong Cave, Yunxi County, Hubei Province. The cave is rich in fossil mammalian fauna and contained stone and bone tools and evidence of butchered bones and fire. The fauna suggest a late Pleistocene date at the latest, while deposits bearing the human teeth have been dated to 44–34 ka BP (by ESR) and 103–79 ka BP (by uranium series), a fairly wide disparity (Liu, Wu, et al., 2010). In general, the morphology and metrics of the teeth are similar to modern humans, although there are some archaic features (such as the robust upper incisors and canine) that are more typical of late Pleistocene humans. The incisors have shoveling and double shoveling and the upper molar has enamel extension, three of eight features that characterize East Asian populations today (Wu et al., 2006; Liu, Wu, et al., 2010).

Jingchuan

In 1976, a human fossil cranium was discovered in Jinchuan County, Gansu Province, in North China. Further field work was done in 2006 to determine the provenience and age of the fossil specimen, which was determined to be 15–48 ka BP based on stratigraphy, fauna, lithics, and OSL dating (Li et al., 2010). The skull has a cranial capacity of 1,524 cc, well within the modern human range, and in general seems quite similar to more recent humans. Nevertheless, the authors see some evidence of archaic features in a principal components analysis comparing the Jingchuan specimen with both archaic and modern humans (Li et al., 2010).

Salkhit

A human skullcap (frontal bone and portions of both parietals) was discovered in Northeastern Outer Mongolia in 2006 during a gold mining operation and is the first known human fossil from the Pleistocene from this region. The fossil is late Pleistocene in age, according to associated faunal remains of woolly rhinoceros. Coppens et al. (2008) described the skullcap as having a mosaic of features, some of which are primitive (well-developed browridges and a keeled frontal squama), some derived (parietal eminences that are posteriorly and superiorly situated, with no sagittal keel), and others Neandertal-like (supratatorial sulcus, prominent glabella, rounded and prominent lateral supraorbital margins, well-defined inward nasion). The authors' multidimensional scaling indicates that Salkhit is quite different from Far East Asian *H. sapiens* fossils and more similar to Neandertals, Chinese *H. erectus*, and West/Far East archaic *H. sapiens*. They tentatively attribute this specimen to archaic *H. sapiens*. Lee and Yi (2012) used the STET method to show that Salkhit and other modern humans from the region belong to the same species as Northeast Asian archaic humans. They argue that this shows that modern humans were not a new, recent species, replacing archaic populations. The fact that Coppens et al. (2008) described the specimen as an archaic *Homo sapiens* while Lee and Yi (2012) referred to it as an early modern human speaks to the mosaic nature of its morphology.

Discussion and Conclusions

The expansion of the fossil record with more and especially better dated specimens allows us to reexamine the hypothesis that Wolpoff et al. put forth in the 1984 chapter that preceded this one. Brown argued (1992, 2001) that although there was clear continuity of morphology and hence of populations in Chinese samples during the Holocene, the sample of material from East Asia was too limited to allow that continuity to be extended back to the middle Pleistocene. For example, at that time the earliest securely dated modern human in East Asia was the Zhoukoudian Upper Cave material dated to a minimum of 29 ky BP. In recent decades, however, much of the Chinese human fossil record has been more rigorously dated using a variety of techniques, including AMS radiocarbon dating and uranium-series. The better dated fossils like Zhirendong and Tianyuan that were excavated systematically and discovered in situ, and often dated directly, provide an improved chronological framework within which we can test models about the nature of human evolution in East Asia. The fact that we find some features of modern humans very early in the fossil record (such as at Zhirendong at 100 ka) and the fact that these features appear as parts of mosaics of features along with more archaic characteristics suggests that modern human morphology did not arrive as a package from outside the region. Finally, the fact that these modern features occur in East Asia so early relative to their appearance in Africa makes it very unlikely that they appeared in East Asia only as the result of gene flow.

The fossil record from China today cannot refute a hypothesis of continuity in the region. Three types of evidence support this assertion: (1) there are features that show continuity in East Asia, meaning that they are more often present in East Asian populations than in other regions, though they are not generally unique to East Asia; (2) there are archaic features that show up in a mosaic fashion in Chinese specimens; and (3) there are morphological features present in East Asian specimens that are more common in other regions of the world and some important shared patterns of evolutionary change. We will discuss features representing these three categories in turn.

1. Features that are rare or absent in African populations:

- Agenesis (congenital absence) of the third molar. This is a feature that had been noted by Weidenreich (1939), Wolpoff et al. (1984), and others as typical of East Asian populations. The feature occurs in the Chenjiawo (Lantian) mandible (Woo, 1964) dating to the Middle Pleistocene, the Liujiang specimen, and in the Tabon mandible from the Philippines. It also occurs in relatively high frequencies in modern populations of the regions, only occasionally in European, and very rarely, if ever, in African populations (Lahr, 1994). These population differences are confirmed by Rozkovcova et al. (1999), who reported frequencies of third molar agenesis up to about 30% in some European populations but only 2.6% and 1.9% in West and East African populations, respectively. Although that paper reported very little data from Asian populations, it did mention two Japanese populations with frequencies of third molar agenesis of 18.4% and 30% and an Aleutian Island population at 40%.
- Pinched nose (present in Upper Cave 101, Maba, Dali, and Nanjing).
- Mandibular torus (present at Locality 1, Zhoukoudian).
- Gabled vault (or sagittal keeling) (present in Ziyang, Locality 1, Zhoukoudian). Lahr (1994: 36) shows that this feature is virtually absent in Africans, virtually absent in Europeans, and occurs in around 9% in East Asians. Wu (2006) argued that this feature (along with mandibular exostoses and third molar agenesis) was strong evidence for the Multiregional Model rather than a Recent Out of Africa model.

Midsagittal keeling and mandibular exostosis, which are seen in East Asians, are also seen in *Homo erectus* from Zhoukoudian, and Lahr (1994: 40) shows that mandibular exostosis is absent in Africans and present in East Asians at a frequency of around 3%. The pinched nasal saddle may be traced to the Maba early *H. sapiens* skull and Upper Cave skull 101; and the agenesis of the third molar is seen in the *Homo erectus* mandible from Lantian and the Upper Pleistocene skull from Liujiang. To consider the origin of these features in recent East Asians as the result of genetic drift after the dispersal of modern humans out of Africa seems implausible. On the contrary, if these features were derived from the African immigrants who replaced indigenous East Asian populations, it is inconsistent for modern humans who would have been the descendants of those replacing populations to exhibit these East Asian features of morphology.

In addition, a number of other features are typically seen in the East Asian human fossil record. These features may not necessarily be independent of one another, and they are not unique to East Asia, but they do not appear together in combination in any single specimen outside of China. These features do not necessarily persist to be more frequent in Holocene specimens from this region, presumably because of stronger gene flow in the later time period.

- Shovel-shaped incisors. Stringer (1992) argued that shovel-shaped incisors are a primitive feature and hence not appropriate for consideration as evidence of continuity. Crummett (1994) showed that the patterns of shoveling in European, African, and East Asian populations were very different in detail. Specifically, in Europe the incisors have evidence of tubercle development, in Africa the crown of the incisor may be curved, and in East Asia, one sees the development of marginal ridges with straight crowns.
- Horizontal fronto-nasal and fronto-maxillary sutures.
- Low flat face.
- High nasomalar angle.
- Flat nasal saddle.
- Quadrangular orbits.
- Round infero-lateral orbital margin.
- Lower margin of cheek bones curved rather than straight.
- Maximum width of vault is at middle third of its length.
- Extrasutural bone at lambda. Before the 1980s, this bone had been shown to be present frequently in early humans from China (Zhoukoudian, Xujiayao, Dali). But it is absent in specimens such as Hexian and Jinniushan, which were found more recently, and is also absent in specimens from the late Pleistocene.
- Anteriorly positioned frontal boss. The position of the most prominent point on the midsagittal contour of the frontal bone shown by an index formed by the nasion subtense fraction (FRF of Howells, 1973) and nasion-bregma chord (FRC of Howells, 1973). Chinese fossils usually exhibit an index between 40 and 50, that is, the position of the most prominent point on the midsagittal contour is at the lower half of the contour, while the indices of Petralona, Kabwe, and Bodo as well as Neanderthals are higher than 50.

In East Asian specimens, the low upper face and the flatness of the face (in the horizontal direction, such as nasomalar angle of the face) as well as the vertical profile of the nasal bones (with the nasal saddle not protruding) provide stronger support for continuity. In China, both earlier and later fossils have a lower upper face and a flatter face, as well as a vertical profile for the nasal bones, while the Middle Pleistocene humans of Africa (e.g., the Kabwe and Bodo specimens) and

Europe (e.g., Petralona) have higher upper faces, which are less flat, along with protruding noses. Rather than considering modern humans of China derived from Middle Pleistocene humans of Africa, we think it is more likely that they evolved primarily from Middle Pleistocene humans of China.

2. Mosaics of archaic and modern features that occur together in Chinese specimens:

Many specimens show a mixture or mosaic of features that make them hard to assign to taxa (either to *Homo erectus*/*Homo sapiens* or archaic/modern humans). For example, the Jinniushan and Dali specimen have been referred to as *Homo erectus* or archaic *Homo sapiens*. The Zhirendong mandible shows a combination of small teeth and various derived features of mandibular morphology with overall mandibular robusticity, generally an archaic feature. The penecontemporaneous specimens from Jinniushan and Dali show a range of cranial vault thickness (thicker in Dali than in Jinniushan). Although it is not common in fossil or extant humans from China, an angular torus occurs in all Chinese *Homo erectus* specimens. It is also present on the Narmada skull from India (Kennedy et al., 1991) Dali, Ziyang and Kow Swamp, and a number of European and African Pleistocene skulls. Some authors, like Wood and Richmond (2000) have argued that the angular torus is an autapomorphy of *H. erectus*. However, we suggest that it indicates the presence of a morphological mosaic between *H. erectus* and *H. sapiens*, showing that there is no clear-cut demarcation between the chronospecies of *H. erectus* and *H. sapiens*.

The Tianyuan Cave remains show a mosaic of derived features such as mandibular and postcranial robusticity and ventral sulcus on the scapula, as well as archaic features of the upper limb such as relatively large lower limb articular surfaces relative to stature.

Importantly, the presence of these mosaics of features goes along with an absence of specimens that possess *only* modern (or only African) features, which is what one would expect under a model of modern human origins that involved replacement of populations from outside the region.

The complicated (mosaic) nature of the transition from archaic to modern *Homo sapiens* in China is itself evidence of the nature of the evolutionary change. That is, the fact that modern features are variable at any point in time and that they appear at different times means that modernity was not something that arrived in China from somewhere else as a single population replacement event. There is certainly no evidence of early modern people in East Asia who have “African” features, which is what one might expect under a replacement scenario. Trinkaus (2005) has made the argument that in Europe and the Near East, early modern human fossils “exhibit complex and varying mosaics of early modern, late archaic, and regional anatomical features” (Trinkaus, 2005: 222). His interpretation is that this reflects a pattern of evolutionary change in which “expanding populations of early modern humans variably absorbed regional late archaic human groups” (Trinkaus, 2005: 222). Although the evidence from East Asia is not as rich or as well dated as the European and Near Eastern fossils, it shows the same pattern of mosaic of features, reflecting a combination of both continuity and gene flow from outside the geographic region.

3. Morphological features that are more common in other regions of the world but that do occur in Chinese specimens:

In addition, there are features that are found occasionally in the Chinese fossil record that are reminiscent of penecontemporary populations in other regions: this includes similarities between the Maba specimen (often referred to as a “Chinese Neandertal”) and European Neandertals (such as the rounded high orbits that are also seen in the Narmada specimen from India), the chignon (occipital bun) in the specimens from Liujiang, Ziyang,

Lijiang, and Chuandong, the Carabelli's cusp in the Lijiang cranium (Carabelli's cusps are very rare in China but much more common in Europe), and the highly protruding nasal saddle and bulge between the anterior nasal aperture and the orbit in the Nanjing 1 and Dali crania that is reminiscent of populations to the west (Wu, 2005). The presence of features that are generally much more common in other regions of the world may be evidence of the existence of persistent gene flow throughout the time period.

Within East Asia (as in Europe and Africa), we also see patterns occurring through time that are part of global patterns of evolutionary change in humans. These include an increase in cranial capacity through the Pleistocene and an overall decrease in cranial and postcranial robusticity and adaptations to climate, which can be seen in the cold-adapted body form of Jinniushan or the more warm-adapted form of Liujiang.

One way to examine the question of gene flow between human populations in different parts of the world is to assess human migration and dispersal in East and Southeast Asia using coefficients of divergence in cranial metrics from specimens from East Asia and neighboring regions. Wu (Wu and Poirier, 1995) showed that the coefficient of divergence between the specimen from Liujiang and specimens from Niah (in Borneo) and Wadjak (in Java) seems to increase as the geographical distance increases, while the specimens from Wadjak and Keilor (in Australia) are relatively similar to each other. This is consistent with the hypothesis that these populations have a prolonged history with substantial gene flow particularly in recent periods.

It is worth noting (although it is a piece of negative evidence) that although individual features that are typical of other regions of the world can be seen in East Asia (such as an occipital chignon in the Chuandong, Liujiang, Ziyang, and Lijiang specimens, the rounded orbits in Maba, the paranasal bulge in Dali, or the very protruding nose in Nanjing 1 and Laishui), no human fossils are known from East Asia that have a *constellation* of distinctively African or any non-Asian morphology. Such fossils, if they existed, could represent early populations from elsewhere in the world that replaced local populations, as would be predicted under a replacement model of evolutionary change in East Asia.

It is our contention that the currently existing human fossil record in China, recently strengthened by well-dated fossils of early modern humans, shows evidence of continuity of what have been described as East Asian features in the cranium, dentition, and occasionally in the less often represented postcrania that suggest a gradual rather than an abrupt trend toward modernity in East Asia. However, importantly, these features do not appear all at once as a "package of modernity" but as an evolutionary mosaic that is consistent with the gradual transition of a population through time and that is *not* consistent with replacement by an outside population. This is what would be predicted under a model of modern human origins that includes both local evolution and gene flow from outside the region and would include models variously called Multiregional Evolution (Wolpoff et al., 1984), Assimilation Model (Smith et al., 2005), or Continuity with Hybridization (Wu, 1998).

In arguing that the fossil record in China shows that large-scale replacement of indigenous populations by modern humans did not occur in East Asia, does that mean that it did not occur in Europe? Wu (1998) argued that different models of modern human origins may occur in different parts of the world (e.g., higher levels of population flow into Europe than into East Asia). He suggested that in China, continuity over time was greater than in Europe, while gene flow from outside regions, though present, was at a lower level of magnitude.

Another issue raised by the East Asian human fossil record is the notion of modernity. We can examine the question of what it actually means to characterize an individual as a modern human. Day and Stringer (1982, 1991) attempted to construct a set of

morphological criteria to define anatomically modern humans (Day and Stringer, 1982, 1991), but that definition was shown to be problematic (Wolpoff, 1986) because it either included some archaic humans not generally thought to be anatomically modern or left out some living humans who are universally recognized as modern. Wolpoff and Caspari's (1996) view of modernity as a cone with the base at the present and fewer modern features being represented as one moves back in time is consistent with the evidence that it is not possible to produce a morphological definition of what it means to be an anatomically modern human. Modernity appeared in China as it did elsewhere in the world, in a mosaic way, appearing trait by trait in different specimens. We agree that the term "modern" should be used as a designation of features, not of populations, because modernity is not universally (globally) defined by particular morphological features and it is not a package of "very successful, interacting anatomical features and behaviors whose genesis is at its origins" (Wolpoff and Caspari, 1996).

Archaeological Record in East Asia

The Chinese archaeological record is another line of evidence that can address the question of whether evolution in this region was characterized by in situ continuity or by an Upper Pleistocene replacement event. As long noted (Movius, 1948), East Asia in general is characterized by a pattern only sporadically showing evidence of bifacial technology ("Mode 2" industries) throughout most of the Pleistocene. Although examples of the latter do occur from a number of regions (most famously from apparent early mid-Pleistocene context in the Bose Valley of southern China [Hou et al., 2000], but sporadically and probably later elsewhere), most Chinese sites through the Middle and early Upper Pleistocene are dominated by Mode 1 lithics, that is, cores with limited flake removal and a low range of flake tools such as scrapers, usually reflecting only moderate retouch. There is wide recognition today that the direct application of the traditional European three-stage Paleolithic sequence is not generally appropriate in China (Gao and Norton, 2002; Shen and Keates, 2003; Norton et al., 2011; Bar-Yosef and Wang, 2012).

Late Upper Pleistocene sites, particularly in northern China, add Mode 4 (blade) and later in some cases Mode 5 (microblade/microlith) technology (Bar-Yosef and Wang, 2012). Importantly and in contrast to patterns in the west, however, there is no systematic progression from the simple chopper or pebble industries of Mode 1 through Mode 5 over time. Examples of Mode 2 industries, where datable, occur at a limited number of locales during a variety of periods (during which Mode 1 continues to dominate at other sites), are rarely or never followed by an elaboration of prepared core flake technology (Mode 3), do not generally develop into Mode 4 technology, and in fact Mode 1 industries remain ubiquitous even through the last 40,000 years. In south China in particular, blade industries (Mode 4 or 5) never became dominant; in North China they apparently spread north to south in the last 40,000 years of the Upper Pleistocene.

Thus, while the appearance of blade and microblade/microlith industries in the late upper Pleistocene may reflect contact or population movement in that period in North China and the sporadic occurrence of other technologies might indicate other episodes of East-West interaction, there is simply no evidence of a technological replacement event corresponding to a putative population replacement, nor does the chronological pattern of technological variation suggest an influx of modern humans replacing East Asian populations in the mid-Upper Pleistocene. The North Chinese lithic changes beginning at some sites around 40,000 BP occur about 20,000 years after the putative arrival of anatomically modern immigrants from Africa in China (Su et al., 1999), and long after specimens such as the Zhirendong mandible

suggest transitional or modern anatomical form. The technological continuity in South China is even more notably at odds with a model of population influx.

Around 100 ka, Mode 3 technology was prevalent in the Middle Stone Age of the Levant and Africa. If the indigenous population of China had been totally replaced by immigrants from Africa, the Paleolithic industries of China should have been totally changed from Mode 1 to Mode 3 or a technology more progressive than these. But there was no such change. There are many more Chinese Mode 1 Paleolithic sites that, while lacking chronometric dates, have been dated to the Late Pleistocene by faunal correlation or geomorphological evidence. So in the period after 60 ka, Mode 1 still constituted the majority of Paleolithic assemblages of China. This pattern in the development of the Paleolithic is inconsistent with a hypothesis of complete population replacement (Wu, 2004).

Summary

In summary, the East Asian record is characterized by (1) the presence and continuation of features that occur in higher frequencies in this region than elsewhere in the world (regionally predominant traits); (2) individual specimens that contain mosaics of primitive and derived features, some of which occur earlier than would be consistent with replacement of indigenous populations by humans from outside the region; (3) the occurrence in East Asia of some morphological features that are generally characteristic of other global regions and (4) no evidence in the archaeological record for discontinuity in the form of change in technology that might signal the influx of a new species or population of humans bringing with them a new technology. Finally, the complicated picture of relationships among ancient and modern people suggested by the new genetic evidence is consistent with an understanding of human evolution within East Asia in which this region represents one stream of the intertwining river of evolutionary change that flows all over the areas of the globe where human habitation occurred.

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This paper is dedicated to the memory of our dear friend and colleague Alan G. Thorne, who passed away as this chapter was being completed. Alan had a longstanding (and infectious!) appreciation for the significance of the East Asian fossil record and its role in understanding human evolution on a global scale. He is deeply missed.

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Note

1. A number of fragmentary (usually dental) remains that are of marginal or no relevance to questions of modern human origins have been omitted. This includes Meipu (fossil teeth discovered in 1974, attributed by Wu and Poirier [1995] to *Homo erectus* and dating to Middle or Early Pleistocene), Bailongdong (teeth discovered in 1977 and attributed to *Homo erectus*), Leiping (fragmentary late Pleistocene cranial base found in the 1950s), Xinglong (a single molar attributed

to *Homo sapiens* and dated to 116–154 K BP), and Xichun (isolated teeth discovered in traditional Chinese medicine pharmacies). This material was all discussed by Wu and Poirier (1995). Migong yielded a late *Homo sapiens* parietal.

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Chapter 4

Perspectives on the Origins of Modern Australians

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Introduction

The study of modern human origins (MHO) in Australasia has a long history. The discovery of the Talgai skull in 1884 is one of the earliest in the history of paleoanthropology, followed only shortly thereafter by Dubois's finds at Trinil 7 years later. Further survey work by Dubois, Oppenoorth, and G. H. R. von Koenigswald on Java is well known and revealed a treasure trove of hominid fossils that would form the bulk of the Indonesian sequence of Pleistocene human evolution. Somewhat less well publicized are the further archaeological discoveries of human remains in Australia throughout the early twentieth century, including the cemetery at Swanport (1911), the Cohuna skull (1925), Keilor (1940), and the large group of skeletons that were recovered by George Murray Black and became known as the "Murray Black" collection. These remains were recovered during a period spanning the late 1930s through the early 1950s and included the series of skeletons from Coobool Creek (Brown, 1982, 1989). Australian archaeologists continued to produce important discoveries of ancient remains through the 1960s and 1970s, including the Kow Swamp and Lake Mungo/Willandra Lakes burials. Unfortunately, work on the prehistory of Australia was significantly impacted in the 1980s by changes in legislation surrounding the ownership of ancient remains (summarized in Pardoe, 2004). Control was transferred to local Aboriginal groups, who reclaimed and reburied many of the Pleistocene human remains recovered by that point (Webb, 1987; Mulvaney, 1991; Pardoe, 2004). It also became much more difficult to publish data or photographs of ancient Australians, as control over the use of any data or images of the fossils also became subject to the discretion of the local Aboriginal groups. As a result, paleoanthropological fieldwork in Australia essentially ground to a halt as much of the modern debate over the origins of modern humans was beginning to take shape (e.g., Thorne and Wolpoff, 1981; Wolpoff et al., 1984; Stringer and Andrews, 1988). While work on some collections of ancient Australian remains (e.g., Roonka, Willandra Lakes) is still possible, there have been no publications on new skeletal material from Australia in decades,

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and analyses of the older material have been few in number. The difficulties encountered in studying Aboriginal remains have led many Australian paleoanthropologists who previously worked on this material to move their research foci to other areas (Pardoe, 2004).

Despite this virtual embargo on new excavations of skeletal material in Australia, the region has continued to receive attention in the debate over MHO. It is often regarded as providing the strongest evidence for in situ evolution of modern humans, and even some advocates of the various replacement models consider Australasia to provide the biggest challenge to those models (e.g., Stringer, 1994). When considering this evidence, however, it is important to be cognizant of the ramifications that the shift in control over the fossils has had for this discussion. For example, many of the key fossils in this debate (e.g., Lake Mungo 3 and WLH 50) have never been formally described in a scientific publication. Several others (e.g., Lake Mungo 1 and the Kow Swamp sample) were described only in Alan Thorne's (1975) dissertation. Many of the repatriated fossils like Cohuna likewise never received a thorough description using modern standards. It is also worth mentioning that the most widely published Australian paleoanthropologist throughout the 1970s and 1980s is Alan Thorne, one of the architects of the modern Multiregional Evolution Model. His work, often in collaboration with Milford Wolpoff, built upon earlier studies by Weidenreich (1943, 1951) and portrayed a portion of the Pleistocene Australian sample as a bridge between the morphology seen in the Ngandong fossils and modern Australians (e.g., Thorne, 1971, 1975; Thorne and Wolpoff, 1981, 1992). It would be difficult to overstate the value of Thorne's contributions to the perceptions of MHO in Australasia, which will be discussed in more detail shortly. As the senior paleoanthropologist in the region, having studied all of the major Australian fossils prior to their return to Aboriginal groups, Thorne was in a unique position to influence the discussion on MHO in Australasia. His many contributions to the scientific literature were quite persuasive and did much to build the perception that the Australian fossil record showed significant evidence that supported the Multiregional Model. In Australia his ideas were further communicated to a broad general audience through the popular television series *Man on the Rim*. Thorne's model, often referred to as the Dihybrid model, posited that two different founding populations had been responsible for the peopling of Australia. This work was both a reaction to and a continuation of earlier migration models that had been proposed by other workers, most notably Birdsell (1949, 1950, 1967).

Birdsell and the Trihybrid model

The initial peopling of Australia has long been a source of fascination. While many early authors, including Turner (1884), Keith (1925), Jones (1934), and Howells (1937), contended that the Australian Aboriginals represented a single, relatively homogenous population, later workers found evidence for multiple founding populations having contributed to the Australian gene pool. Morrison (1967) postulated that two successive waves of migrants had populated the continent, based on gene frequency data. More widely known, and discussed, were Birdsell's (1949, 1950, 1957, 1967, 1977) ideas alleging that three different founding populations formed the ancestry for Aboriginal Australians. Birdsell (1949, 1967) rejected earlier studies supporting a single founding population because they were based primarily on cranial studies. His work, on the other hand, incorporated an enormous dataset collected from living populations representative of diverse environments, including anthropometric data, skin and eye pigmentation, hair color and type, dental morphologies, and blood groups (Birdsell, 1949, 1950, 1967).

According to this Trihybrid origin model (Birdsell, 1967), the three ancestral groups that initially inhabited Australia were the Negritos (sometimes referred to as Barrineans), Murrayians, and Carpentarians. The Negritos were thought to be the first group to arrive,

and these people were characterized by short stature, dark skin, woolly hair, and a short and narrow face (Birdsell, 1950). They were followed by the Murrayian people, who were likewise short in stature but had lightly pigmented skin, wavy to straight hair, and large faces with big browridges (Birdsell, 1950). The taller Carpentarians arrived last, with darker pigmentation in their skin, wavy to straight hair, and a high and narrow skull with large brows (Birdsell, 1950). Birdsell (1949, 1950, 1967) contended that most of the Negrito contribution to the early Australian gene pool had been swamped by the subsequent arrivals of the later groups, and only very few marginalized populations remained. Meanwhile, the descendants of the Murrayians settled primarily in the southern part of the continent while the Carpentarians claimed the north (Birdsell, 1967). While much of the data used to support these categorizations was obtained from extant groups, recently discovered fossils were also incorporated into his hypothesis. The so-called “Deep” skull from Niah Cave was found to “(contain) the blending of the same racial elements found in those (Tasmanian) Aborigines, namely Oceanic Negrito, and Murrayian Australian” (Birdsell, 1967: 103). Likewise, the Keilor skull was found to be “classic Murrayian in type” (Birdsell, 1967: 148) and the Wajak 1 skull from Java was also placed in this grouping. Additionally, three distinct cultural sequences were identified by Tindale (1957) in the archaeological assemblages at Devon Downs, and these were likewise thought to provide evidence for distinct migrations to Australia.

While criticized by Abbie (1951, 1963, 1966) and later by others (e.g., Howells, 1973a, 1973b, 1977; Larnach, 1974; Macintosh and Larnach, 1976; Thorne, 1977), Birdsell’s (1949, 1950, 1967) model was influential. Indeed, it is still occasionally resurrected even today (e.g., Windschuttle and Gillin, 2002; see Westaway and Hiscock, 2006, and Grounds and Ross, 2010, for rebuttals). These ideas were an unfortunate product of an unfortunate time, when morphological differences were often portrayed through racial typologies and the idea of “pure racial strains” was common in anthropological studies (Howells, 1977). The publication of Carlton Coon’s (1962) *The Origin of Races*, and the dismal reception the book received, signaled a significant shift in the approach to understanding human diversity. As the 1960s progressed, Birdsellian models explaining morphological change through hybridization of different racial groups were typically replaced by more nuanced ideas that invoked drift, selection, and local adaptations to explain the changes seen in the fossil and archaeological records.

Thorne and the Dihybrid Model

Alan Thorne (e.g., 1971, 1976, 1977, 1980, 1981, 1989, 2002; Thorne and Macumber, 1972; Thorne and Wolpoff, 1981, 1992) has likewise invoked migrations of different populations to Australia as a means of explaining the anatomical diversity present in the fossil record. This model was developed through the acquisition of new skeletal material from excavations at Kow Swamp and Lake Mungo. These excavations dramatically increased the available dataset in Australia from just a few isolated crania to several more complete individuals. While Birdsell’s ideas had been developed through work with living people, Thorne was working with skeletons that were thought to date to near the initial peopling of the continent. Another distinction between the models is that Thorne’s Dihybrid model emphasizes *morphological* variation and not racial typologies. This is an important difference from Birdsell’s (1949, 1950, 1967) ideas concerning the blending of racial strains.

Thorne’s writings on MHO in Australia were developed after he undertook excavations at Kow Swamp and participated in the excavations at Lake Mungo (Thorne, 1971, 1975; Thorne and Macumber, 1972; Bowler and Thorne, 1976). The Lake Mungo 1 (also sometimes referred to as Willandra Lakes Hominid [WLH] 1) skeleton (Bowler et al., 1970, 1972),

discovered in 1968, is exceptionally lightly built, with a rounded forehead and no browridges, and this gracility contributed to the skeleton being identified as female. Another skeleton located approximately 500 m from Lake Mungo 1 was found in 1974 and was designated Lake Mungo 3 (sometimes WLH 3) (Bowler and Thorne, 1976). This latter skeleton shared the light build of Lake Mungo 1 but was thought to represent a male based on the morphology of the pelvis and the positioning of the body in the grave (Bowler and Thorne, 1976). Accidental discoveries of skeletal material at Kow Swamp began as early as 1962 (West, 1977), and work at the site between 1968 and 1973 uncovered a total of twenty-two burials complete enough to be assigned individual numbers, plus hundreds of additional bone fragments and teeth that could not be assigned to any of the numbered individuals (Thorne and Macumber, 1972; Thorne, 1975). The specimens from Kow Swamp were all quite heavily built, with thick cranial bone, large browridges, and flatter frontals with significant postorbital constriction (Thorne and Macumber, 1972). These morphologies provided a stark contrast to the individuals found at Lake Mungo, and Thorne (1971, 1975, 1980) was impressed by the level of morphological differences he saw. These skeletons formed the basis for the “robust” and “gracile” dichotomy espoused by the DiHybrid model, and other specimens like Keilor, Green Gully, King Island, and Lake Tandou joined the Lake Mungo skeletons in the “gracile” group (Figure 4.1), while Cohuna, Cossack, Mossiel, WLH 50, and the Coobool Creek sample were put in the “robust” group (Figure 4.2) (Freedman and Lofgren, 1979; Thorne, 1980, Habgood, 1986; Sim and Thorne, 1990; Thorne and Wolpoff, 1992).

Thorne (1980: 40) claimed that the “robust” group had “the mark of Ancient Java,” while the “gracile” Australians showed “the stamp of ancient China.” Javan fossils from Sangiran and Ngandong were identified as representatives of the regional evolutionary sequence, sharing a number of features with the “robust” Pleistocene Australians, including thick cranial bone, low and sloping foreheads, large browridges with development of lateral trigones, and facial prognathism (Thorne, 1977, 1980; Thorne and Wolpoff, 1981). Conversely, Chinese fossils like the Zhoukoudian Upper Cave crania and the Liujang skull provided examples of the predecessors of the more “gracile” Australians (Thorne, 1980). These crania all show more delicate features like thinner bone, higher foreheads, and minimal browridge development. Specimens like the Niah Cave “Deep” skull, the Tabon skull in the Philippines, and the Wajak specimens from Java provided evidence of the spread of this gracile morphology closer to Australia (Thorne, 1980).

Thorne’s arguments (1971, 1977, 1980, 1981) found support from Milford Wolpoff, resulting in a rich collaboration that explained the origins of modern humans through multiregional continuity (e.g., Wolpoff et al., 1984; Thorne and Wolpoff, 1981, 1992). Indeed, the Australian record contributed substantially to the formation of the modern Multiregional theory of MHO. In Australasia, this idea could trace its beginnings to Weidenreich’s (1943: 276) famous statement that “there is an almost continuous line leading from *Pithecanthropus* through *Homo soloensis* and fossil Australian forms to certain modern primitive Australian types.” The “robust” Australians like Kow Swamp and WLH 50 seemed to fit Weidenreich’s assertions perfectly and filled in a temporal gap between the Ngandong crania and modern Australians. The presence of the more “gracile” fossils like those from Lake Mungo did present a problem with this scenario but were explained by the influx of more lightly built people from northern Asia. Thus, Australia seemed to fit well with the notion that “various features of modern humans had separate roots in different regions, and that these features spread by gene flow and population movements until they prevailed” (Wolpoff, 1999: 563).



Figure 4.1. Some crania belonging to the “gracile” group of early Australians: Keilor (left) and Lake Mungo 3. Both specimens are casts.



Figure 4.2. Some crania belonging to the “robust” group of early Australians: Cohuna (upper left), Kow Swamp 5 (upper right), and WLH 50. All specimens are casts.

Single Population Model

While hypotheses invoking multiple founding populations for Aboriginal Australians have often received most of the attention in the literature, there is an equally long history of support for the hypothesis that a single founding group initially populated Australia (e.g., Abbie, 1951, 1963, 1966; Howells, 1973a, 1977; Larnach, 1974; Macintosh and Larnach, 1976; Habgood, 1986; Pardoe, 1991, 2006; Brown, 1987, 1994, 2000). Through their work on modern crania both Howells (1973a, 1977) and Larnach (1974) found Australian samples to be homogenous. Multivariate work by Habgood (1986) also questioned the validity of Thorne's Dihybrid scenario, finding that late Pleistocene/early Holocene Australian crania tended to cluster with one another and away from other regional populations. Work by Pardoe (1991, 2006) and Brown (1987, 1989, 1994, 1995, 2000) also supports the notion that there is little to no evidence to support hypotheses of multiple founding populations in Australia.

As mentioned earlier in this chapter, Thorne's ideas have essentially framed the debate over MHO in Australasia, and subsequent work by scholars interested in the area has been focused on examining his claims in more detail. This work has generally centered on two key lynchpins of his theory: the existence of separate "robust" and "gracile" founding populations, and the Javan ancestry of the "robust" early Australians.

Multiple Migrations?

In a review article, Pardoe (1991) describes the various hypotheses that have been proposed to explain the patterns of robusticity in Australia as either "migrationist," "selectionist," or "bio-culturalist." The migrationist viewpoint is best exemplified by the writings of Thorne (1976, 1977, 1980, 1981, 1984, 1989, 2002; Thorne and Wolpoff, 1981, 1992) and Webb (1989, 2006). This viewpoint seeks to explain variation in early Australians primarily through an influx of morphologically different founding populations. The selectionist arguments (e.g., Brown, 1987, 1989; Bulbeck, 2001) contend that variation in early Australians can be explained through selective pressures caused by changes in climatic and environmental conditions throughout the late Pleistocene and early Holocene. Other possible explanations for the variability in early Australians hinge on bio-cultural factors, most notably interpersonal violence (e.g., Brown, 1989) and artificial cranial deformation (e.g., Brothwell, 1975; Brown, 1981, 1989, 2010; Antón and Weinstein, 1999; Durband, 2008a,b) that can influence the development of cranial vault form and thickness.

The validity of the migrationist viewpoint hinges on the notion that the "starkly contrasting robust and gracile individuals . . . makes the one range of variation arguments untenable" (Webb, 2006: 233). One difficulty with this argument, that has received little notice, is the lack of agreement between authors as to the group memberships of the "robust" and "gracile" categories. For example, Thorne (1977, 1980) places the Lake Nitchie skull into his "robust" group, while Howells (1973a) puts it into the "gracile" group. Habgood (1986) also struggled with the placement of Lake Nitchie into either grouping. This specimen has been difficult to classify satisfactorily at either end of the dichotomy, because while it is a large cranium it also has more "gracile" features like a high and rounded forehead and smaller face (Habgood, 1986, 2003; author's observations). Keilor has likewise typically been classified as "gracile" (Thorne, 1977, 1980), but it is also a large and anatomically robust cranium (Brown, 1987, 1989; Wolpoff, 1999; author's observations). In some measures the Lake Tandou cranium fits well with "gracile" crania like Keilor and Lake Nitchie, but the former specimen's cranial bone thickness and dental dimensions are more similar to "robust"

specimens (Freedman and Lofgren, 1983; Habgood, 1986). Webb (1989, 2006) contends that separate “robust” and “gracile” groups are well represented in the Willandra Lakes sample, but Pardoe (1991, 2006) has persuasively argued that these differences in robusticity are simply a misidentified pattern of normal sexual dimorphism (Hiscock, 2008). Brown (1994, 1995) also disputes the sex of the King Island skeleton, another individual classified as “gracile” (Sim and Thorne, 1990), and the attribution of male sex to the “gracile” LM3 (Brown, 2000; though see Durband et al., 2009). Finally, Wolpoff (1980) stated that the samples from Lake Mungo and Kow Swamp, typically seen as representing the two extremes of the “robust” and “gracile” groups, overlap considerably. Indeed, “the (morphological) range at a single site (Kow Swamp) encompasses most of the known fossil material” (Wolpoff, 1980: 330). While there are clearly some robustly built individuals in the Australian fossil sample, most notably WLH 50 (who will be discussed in more detail below), the “robust” and “gracile” dichotomy is considerably muddier than it is often portrayed.

Habgood (1986: 134) demonstrated that the early Australian cranial sample represented “a single, but morphologically variable, population.” While there may be some differences in cranial size between the late Pleistocene and early Holocene Australians, there are no significant differences in cranial shape between the “robust” and “gracile” samples (Habgood, 1986). Dental and mandibular dimensions from the “robust” Kow Swamp sample likewise generally fall within the modern Australian range, and when they do exceed that range they do so only fractionally (Freedman and Lofgren, 1979; Habgood, 1986; though see work by Brown, 1987, 1989, 2000). Postcranial analyses have also found considerable overlap between so-called “robust” and “gracile” individuals (Durband et al., 2009).

While the “migrationist” theory for explaining cranial variation in Australia appears to be weak, there are possible alternatives to explain not only the levels of robusticity seen in Australia but why the patterning of robusticity in early Australian populations appears to run counter to the reduction in robusticity throughout the late Pleistocene/early Holocene seen in virtually all other areas of the world. The “bio-culturalist” viewpoint posits that various cultural influences have accentuated cranial robusticity in some early Australians. Brown (1989) has found evidence for higher levels of interpersonal violence and has suggested that these cultural practices could have led to selection for thicker cranial vaults. Selection focused on thickening vault bone could explain why some early Australian groups developed heavier skulls and would also be consistent with other results suggesting that there is very little difference between “robust” and “gracile” individuals postcranially (Durband et al., 2009). An additional cultural practice that appears to have influenced the “robust” appearance of several oft-mentioned individuals in this debate is artificial deformation of the skull (Brothwell, 1975; Brown, 1981, 1989; Antón and Weinstein, 1999; Durband, 2008a,b). In general, the “robust” Australian crania that look the most archaic, like Cohuna and Kow Swamp 1 and 5, have been shown to share strong shape similarities with known artificially deformed crania (Brown, 1981, 1989; Antón and Weinstein, 1999; Durband, 2008b). Many additional specimens from Coobool Creek and elsewhere have cranial vault shapes that are consistent with artificial deformation (Brown, 1989, 2010; Durband, 2008a). This practice produces a low, sloping frontal bone and also influences the development of non-metric features like the browridges (Brown, 1989). These cultural influences have served to heighten, and potentially manufacture, many of the apparent differences in robusticity seen in early Australian groups along the Murray River.

The “selectionist” hypothesis contends that the changes in robusticity in Australia are due primarily to localized climatic and environmental conditions. Brown (1987) and Bulbeck (2001) have argued that increasingly harsher climates during the Last Glacial Maximum in Australia would have led to increased robusticity and body size amongst Pleistocene Australians. While Bulbeck (2001) did not specify a mechanism responsible for this increased

robusticity, Westaway (2009) found that maximum cranial robusticity in the Willandra Lakes correlates with the time period of the Last Glacial Maximum. As the climate ameliorated into the Holocene, smaller body sizes and reduced robusticity would have become the norm (Brown, 1987). Selection and adaptation can also explain differing levels of robusticity in the skeletal sample. Processes like Bergmann's rule led to more lightly built bodies and skeletons in populations living in warmer and more arid environments, like those around Lake Mungo (Pardoe, 2006). Likewise, more temperate environments and ample resources around the Murray River would contribute to the development of more robust individuals (Pardoe, 2006). Demographics would have further influenced selection in areas like the Murray River Valley, where population densities would have been considerably higher (Pardoe, 1993, 2006; Hiscock, 2008). More complex demographic and social relationships in higher-density areas provided mechanisms to restrict gene flow among various early Australian populations (Pardoe, 2006; Hiscock, 2008), leading to culturally determined patterns of mate exchange that would have influenced patterns of skeletal development. Pardoe (2006) contends that riverine groups like those at Kow Swamp and Coobool Creek would have become more genetically secluded despite higher population densities in the area. While this may seem counter-intuitive, Pardoe (2006) argues that strong social and territorial organization influenced the inclusion or exclusion of suitable mates, thereby limiting gene flow and leading to stronger levels of skeletal differentiation (Hiscock, 2008). Cultural practices like artificial deformation along the Murray River provide potential evidence of these group distinctions (Hiscock, 2008), and the interpersonal violence noted by Brown (1987) is consistent with increased population densities and unfriendly intergroup interactions as well.

Based on this evidence it would appear that support for a "migrationist" model to explain cranial variability in early Australian groups (e.g., Thorne, 1971, 1977, 1980; Webb, 2006) is not strong. Instead, the observed range of biological variation can be accounted for by localized evolutionary processes combined with cultural factors like mate selection that would increase the potential for genetic drift. Additionally, cultural phenomena such as interpersonal violence and artificial cranial deformation also influenced cranial shape and thickness, accentuating some regional distinctions between populations. In short, a single origin model for the Australians, combined with the effects of selection, is perfectly consistent with the evidence and presents a parsimonious scenario.

Evidence for Javan Ancestry in Ancient Australians?

Though one of Thorne's tenets, that of multiple migrations, has been weakened, this does not necessarily reduce the likelihood of his second tenet, that of a strong Javan component in the early Australian gene pool. These arguments have been more recently championed by Webb (2006). Evidence for continuity with local archaic groups would be consistent with both the strict Multiregional Model (e.g., Wolpoff, 1992; Hawks et al., 2000; Wolpoff et al., 2001) and the Assimilation Model (e.g., Smith et al., 1989; Smith, 1992, 2010; Cartmill and Smith, 2009) of MHO. Indeed, since Weidenreich's (1943, 1951) work, the perception has been that Indonesian fossils from Ngandong exhibited clear similarities with modern Australians, and these arguments were thought to be strong enough to "(represent) the greatest challenge to the Out of Africa model" (Stringer, 1992: 15).

A number of different characteristics have been argued to demonstrate regional continuity in Australasia, and these have been focused on similarities between Indonesian *Homo erectus* from Sangiran and Ngandong (note that some workers refer to the Ngandong specimens as *Homo soloensis*, e.g., Zeitoun, 2002; Durband, 2004, 2007, 2008c; Webb, 2006) and the "robust" early Australians, particularly individuals from Kow Swamp and the enigmatic

WLH 50. Various work has noted continuity in facial features (e.g., Thorne and Wolpoff, 1981), mandibular morphology (e.g., Kramer, 1989, 1991), and characteristics of the cranium, including the vault and base (e.g., Weidenreich, 1951; Thorne, 1971, 1977, 1989, 2002; Thorne and Wolpoff, 1981; Wolpoff, 1992; Frayer et al., 1993; Hawks et al., 2000; Wolpoff et al., 1984, 2001; Curnoe, 2007) and has contributed to the perception that there is a strong case for continuity in the region. These papers have been countered by some alternative interpretations of the data (e.g., Stringer and Andrews, 1988; Brown, 1989, 1992; Stringer and Bräuer, 1994; Baba et al., 2000; Bräuer et al., 2004; Durband, 2004, 2007, 2008c, 2009; Westaway and Groves, 2009), and a reanalysis of the case for regional continuity is warranted.

While Thorne and Wolpoff (1981) found some evidence for continuity between Sangiran 17 and late Pleistocene Australians in the cranial vault, they argued that facial similarities provided better evidence for a clade relationship in the region. The facial features allegedly held in common between Sangiran 17 and Kow Swamp/Cohuna include marked facial prognathism, eversion of the lower border of the malar, a malar tuberosity, rounding of the infero-lateral border of the eye orbit, and facial/dental reduction (Thorne and Wolpoff, 1981: 342–345). Those authors recognized that these features could be found singly in other specimens of the genus *Homo* but claim that no other regional groups would show them in combination as seen in Australasia (Thorne and Wolpoff, 1981). Habgood (1989, 2003) found that many of the traits identified by Thorne and Wolpoff (1981) can be commonly found throughout samples of *H. erectus* or *H. sapiens*, but argues that a subset of these traits in combination supports the notion of regional continuity. In particular, facial prognathism, a long and sagittally flat frontal bone with a posterior position of minimal frontal breadth, a medium-to-marked malar tuberosity, and the eversion of the lower border of the malar were identified by Habgood (2003) as a combination of traits that could be unique to Australasia.

A number of other authors have pointed out several difficulties with these alleged regional traits. Brown (1992) notes that facial prognathism was fairly common throughout the late Pleistocene and is also influenced by dental function and thus a poor choice for a phylogenetically informative trait. More problematic for arguments of regional continuity hinging on Sangiran 17 is a new reconstruction of the fossil done by Baba and colleagues (1998, 2000). When the skull was originally discovered the facial region was pushed posteriorly and superiorly underneath the braincase (Sartono, 1975) and was subsequently reconstructed by Wolpoff (e.g., Thorne and Wolpoff, 1981). The new reconstruction by Baba and colleagues (1998, 2000) further reorganized and stabilized the skull and reconstructed the left side of the face. Following this reconstruction these authors reevaluated the facial traits identified by Thorne and Wolpoff (1981) and found that the “Sangiran 17 face does not possess the marked facial prognathism, rounding of the inferolateral border of the orbit, malar tuberosity, and steep curvature of the posterior alveolar plane” (Baba et al., 2000: 62). They conclude by stating that “so far as the facial morphological characters are concerned, the regional continuity in Australasia is far less evident than Thorne and Wolpoff (1981) argued” (Baba et al., 2000: 62). Since Sangiran 17 is the only Indonesian *H. erectus* specimen that retains any portion of the lower facial skeleton (Durband, 2009), these questions about its morphology cause significant problems for claims of regional continuity made by both Thorne and Wolpoff (1981) and Habgood (2003).

Brown (1981) and Kramer (1989, 1991) described evidence for regional continuity in mandibles. While Brown (1981) found fault with several cranial traits mentioned by Thorne and Wolpoff (1981) as being indicative of continuity in Australasia, he did argue that some characteristics of the oro-facial complex may still support regional continuity. Kow Swamp and Coobool mandibles show high levels of overall robusticity, great symphyseal height, rami that were tall relative to mandibular length with broad condyles and high arched coronoids, marked gonial eversion, deep masseteric fossae, great bigonial breadth, a high and negative

chin, and extremely pronounced lateral prominences (Brown, 1981: 166). Groves (1989) and Habgood (2003) point out that all of these traits are either generally characteristic of *H. erectus* or plesiomorphic. Kramer (1989, 1991) found that the mandibular sample from Sangiran shares a plurality of features with modern Australians to the exclusion of a robust modern African sample. Habgood (2003) likewise highlights some methodological flaws with that study, citing the lack of other ancient or modern comparative samples and the conflation of some data obtained from published sources. The absence of any ancient Australian data in Kramer's (1989, 1991) samples is also regrettable, though understandable given the political climate surrounding those remains when he was performing the work. In sum, however, the mandibular data supporting regional continuity in Australasia is problematic.

While the aforementioned facial and mandibular data have formed a part of the argument for regional continuity, cranial features have predominantly been the focus (e.g., Thorne, 1971, 1976, 1977; Thorne and Macumber, 1972; Frayer et al., 1993; Habgood, 1989; Groves, 1989; Lahr, 1996; Hawks et al., 2000; Wolpoff et al., 1984, 2001). The form of the browridges and presence of a lateral supraorbital trigone have long been mentioned as continuity features in Australasia (Thorne, 1971; Thorne and Macumber, 1972; Webb, 1989; Lahr, 1996; Wolpoff, 1999; Hawks et al., 2000; Wolpoff et al., 2001; Curnoe, 2007). Browridge form is actually quite different between the Ngandong and Australian samples, however, with each group showing a different pattern of browridge development (Webb, 1989; Durband, 2009). The Ngandong crania all show browridges that are straight and bar-like, with thinner medial segments and much thicker lateral segments that terminate at the knob-like lateral supraorbital trigone (Webb, 1989; Durband, 2009). "Robust" Pleistocene Australians, such as the Kow Swamp sample or WLH 50, have a different pattern of browridge development, with a thicker medial segment and thinner lateral segments, and their brows are curved above each orbit (Webb, 1989; Durband, 2009). These differences in overall browridge morphology are often ignored due to a focus on the lateral corner of the brows at the supraorbital trigone (though see discussion in Webb, 2006). Even here, though, it is difficult to find similarities between the Ngandong fossils and early Australians that are more than superficial. The development of the supraorbital trigones in ancient and modern Australians does not differ from those seen in other modern human groups outside the region. Lahr (1996: 143–144) found that "a pronounced (supraorbital) trigone may be considered the ancestral condition for modern humans" and that Ngandong showed "different structural characteristics" in this feature from all modern human groups. These features fail to provide evidence for continuity in Australasia.

Other characteristics of the frontal bone have also been highlighted by advocates of regional continuity between the Indonesian and early Australian samples. These include frontal flatness (e.g., Thorne, 1971; Thorne and Macumber, 1972; Frayer et al., 1993; Wolpoff, 1999; Curnoe, 2007), sagittal keeling on the frontal (e.g., Hawks et al., 2000; Wolpoff et al., 2001; Curnoe, 2007), and a prebregmatic eminence (Hawks et al., 2000; Wolpoff et al., 2001; Curnoe, 2007). As with the claims for the browridges, the evidence for continuity in these features has also been shown to be problematic. As mentioned above, many of the "robust" early Australians have been shown to be affected by artificial cranial deformation (e.g., Brothwell, 1975; Brown, 1981, 1989, 2010; Antón and Weinstein, 1999; Durband, 2008a,b). This modification would have created the appearance of a flatter frontal bone than would have been normal for these groups. While it is certainly true that only a portion of the early Australian sample has been demonstrated to have been modified in this manner, the list of crania that have the strongest evidence for modification (e.g., Cohuna, Kow Swamp 1 and 5; Brown, 1989; Antón and Weinstein, 1999; Durband, 2008b) are among the crania most often mentioned as having the strongest similarities with Indonesian *H. erectus* (e.g., Thorne, 1971; Thorne and Macumber, 1972; Wolpoff, 1999; Habgood, 2003; Curnoe, 2007). While

WLH 50 does not appear to have been artificially deformed, its cranial vault profile is also likely anomalous due to pathology (e.g., Webb, 1989, 1990, 1995; Brown, 1989), and this specimen is far from representative of the typical early Australian (see discussion below). Other specimens noted by Habgood (2003: Table 6:5) as showing frontal flatness are either in such poor shape that their true form is difficult to determine (Talgai) or affected by either postdepositional distortion (Cossack) or probable artificial deformation (Mossgiel). It is also worth noting that none of these studies identified any “gracile” Australians as having a flatter frontal bone. The prebregmatic eminence can be influenced by artificial cranial deformation (Brown, 1989), and thus its presence in some early Australians with very low frontal squamae is not unexpected. As for sagittal keeling on the frontal bone, both Santa Luca (1980) and Rightmire (1990) found this feature to be variable in the Ngandong sample. Thorne (1976: 100) also notes that Kow Swamp 9 “is the only individual (of 10) to display keeling or gabling on the vault. All other Kow Swamp crania are rounded across the sagittal suture.” In short, none of these commonly cited features on the frontal bone appear to be strong indicators of regional continuity.

On the parietal bones, features like the presence of a sagittal keel (Frayer et al., 1993; Hawks et al., 2000; Wolpoff et al., 2001) and an angular torus (Frayer et al., 1993; Wolpoff, 1999; Hawks et al., 2000; Wolpoff et al., 2001; Curnoe, 2007) have been alleged to be indicative of regional continuity in Australasia. As mentioned above, keeling is present in only 10% of the Kow Swamp series (Thorne, 1976) and is variable on the Ngandong skulls (Rightmire, 1990). Angular tori are likewise variable in earlier Indonesian *H. erectus* (Santa Luca, 1980; Rightmire, 1990; Habgood, 2003; though see Grimaud-Herve, 1986) and can be found on hominids outside of Australasia (e.g., Bräuer and Mbua, 1992). While some “robust” early Australian crania are said to show an angular torus (e.g., Thorne and Macumber, 1972; Hawks et al., 2000), this trait is variable and seems to differ from the form seen in Indonesian *H. erectus* (Habgood, 2003). Other difficulties with these traits are provided by Bräuer and colleagues (2004).

Characteristics on the occiput have also been mentioned frequently in studies purporting to demonstrate regional continuity in Australasia, including the presence of a nuchal torus, a suprainiac fossa, a projecting inion, and a postlambdoidal eminence (Thorne, 1971; Thorne and Macumber, 1972; Frayer et al., 1993; Hawks et al., 2000; Wolpoff et al., 2001; Curnoe, 2007). Earlier work focused on these features in the Kow Swamp sample (e.g., Thorne, 1971; Thorne and Macumber, 1972; though also see Curnoe, 2007), while more recently a focus on the enigmatic WLH 50 has been applied to this problem (e.g., Frayer et al., 1993; Hawks et al., 2000; Wolpoff et al., 2001). While there have been some significant methodological questions raised about these latter projects (Bräuer et al., 2004), even if taken at face value, the utility of these features is questionable at best. With the nuchal torus, for example, the Ngandong fossils show a very characteristic, potentially unique, morphology of a strong bar-like transverse torus that overhangs a nuchal plane with a “scooped out” appearance. None of the “robust” early Australians has a nuchal area that approaches this morphology, nor even qualifies as a true nuchal torus as seen on earlier specimens of Indonesian *H. erectus* from Sangiran. While there is a strong development of the superior nuchal line, this does not differ from the morphology seen in modern humans from other areas. Even the hyper-robust WLH 50 does not show a bar-like torus as seen in Ngandong, nor does that individual have the “scooped out” appearance of the nuchal plane based on the surviving, and significantly eroded, morphology. The use of the suprainiac fossa as a continuity feature in Australasia is problematic on two fronts. First, many of the key specimens that have been cited as having a suprainiac fossa, like Kow Swamp (Thorne and Macumber, 1972) or WLH 50 (Hawks et al., 2000) have an occipital that is postdepositionally distorted (Kow Swamp 1; Durband, 2008b), probably influenced by

artificial deformation (Kow Swamp), or significantly eroded (WLH 50). Further, recent work by Balzeau and Rougier (2010) indicates that a suprainiac fossa can be caused by a variety of phenomena and is thus unlikely to be phylogenetically informative. A strong inferiorly projecting process at inion is also characteristic of the Ngandong fossils and has likewise been said to be found on WLH 50 (e.g., Frayer et al., 1993; Hawks et al., 2000; Wolpoff et al., 2001). As with the rest of the nuchal torus, inion is significantly eroded on WLH 50, but even with this erosion it is clear that inion would not have the same strongly projecting, inferiorly pointing triangle morphology seen in Ngandong. An uneroded example of a similar morphology can be seen on WLH 130 (classified as “gracile” by Webb, 2006) or the slightly damaged occipital of WLH 19. The undescribed WLH 152 individual mentioned by Webb (2006), a heavily built individual similar to WLH 50 in many cranial features, shows a well-developed external occipital protuberance in that area and not a Ngandong-like triangle at inion. If WLH 50 were not eroded, it would almost certainly correspond closely to these examples. A postlambdaid eminence visible in a lateral view (e.g., Frayer et al., 1993; Hawks et al., 2000; Wolpoff et al., 2001) is said to be another similarity between the Ngandong fossils and some early Australians. However, the postdepositional distortion to the occipital of Kow Swamp 1 (Durband, 2008b), and the artificial deformation of the skull in other specimens from Kow Swamp and Cohuna (e.g., Brown, 1989; Antón and Weinstein, 1999; Durband, 2008b), would have had an influence on the development of this feature. Pathology is a concern for WLH 50 (Webb, 1989, 1990, 1995; though see Hawks et al., 2000).

Conspicuously absent from these aforementioned discussions of features supporting regional continuity in Australasia are a number of features that have been identified as unusual and apparently autapomorphic on the Ngandong occipitals. These features include the postcondyloid tuberosities, large rugose bulges at the posterior end of the foramen magnum flanking either side of opisthion. First identified by Weidenreich (1951), subsequent work has indicated that these tuberosities are not developed in fossil or modern Australians or any other modern groups (Durband, 2004, 2007, 2009). The posterior foramen magnum of the Ngandong hominids narrows to a point, a feature known as an opisthionic recess, and this morphology gives the foramen magnum of the Ngandong crania a distinctive teardrop shape (Baba et al., 2003; Durband, 2004, 2007). This feature is quite rare in modern humans from any region (Durband, 2007) and does not appear in any fossil Australians, including the Kow Swamp individuals. The orientation and size of the occipital condyles in Ngandong are also unusual when compared to modern humans (Weidenreich, 1951; Durband, 2004, 2007, 2009). The occipital condyles of Ngandong 7 (Solo 6) are oriented parallel to the midline, rather than tapering toward the midline at the anterior end as in most modern humans. Weidenreich (1951) reconstructed a similar orientation in Ngandong 12 (Solo 11). Of the fossil Australians, only Kooragang shows this condyle orientation (Durband, 2004). The occipital condyles in Ngandong are also quite small relative to the size of the foramen magnum (Durband, 2004, 2007) and show size ratios that are rarely matched in modern humans (Durband, 2007). These features are consistently seen on all the Ngandong crania that preserve these areas and are thus likely to be the typical conditions for these people. These traits should therefore be quite informative for the debate over regional continuity in Australasia. The fact that these characteristics are apparently peculiar to Ngandong, and do not appear in early Australians or any other fossil or modern groups, casts further doubt on the probability of continuity between Ngandong and early Australians.

Other apparently autapomorphic features of the cranial base in the Ngandong series include the location of the squamotympanic fissure in the mandibular fossa (Durband, 2002, 2008c) and the morphology of the foramen ovale (Weidenreich, 1951; Jacob, 1969; Baba et al., 2003; Durband, 2007). The Ngandong crania (including Sambungmacan and Ngawi) all show a squamotympanic fissure that runs wholly in the roof of the mandibular

fossa and do not show development of an inferiorly projecting postglenoid tubercle immediately anterior to that fissure (see discussion in Durband, 2008c). This unique morphology appears to be isolated to the fossils from Ngandong and Sambungmacan 1 and 3 (Durband, 2002, 2008c;), with a somewhat transitional morphology in Sambungmacan 4 (Baba et al., 2003). None of the fossil or modern Australians show this configuration in the mandibular fossa (see Thorne, 1975, and Thorne and Macumber, 1972), and it appears to be autapomorphic for Ngandong (Durband, 2002, 2007, 2008c). Weidenreich (1951) first noted the unique nature of the foramen ovale in the Ngandong fossils. In these specimens, the foramen is divided in two by a broad septum, and these two foramina are located at the base of a deep pit (Weidenreich, 1951; Jacob, 1969). The ovale septum is broken on the right side of Ngandong 7 (Jacob, 1969; author's observation), leading Weidenreich (1951: 281) to misattribute the ovale septum to "three of the four skulls" when it was actually present on *three of the four foramina* (bilaterally in Ngandong 7 and 12) that were preserved. Ovale septa have since been noted on Sambungmacan 4 as well (Baba et al., 2003). As with the other potential autapomorphies discussed for Ngandong, this seemingly unique morphology of the foramen ovale has not been seen in ancient or modern Australians (see Thorne, 1975) nor other fossil or modern human groups (Durband, 2004, 2007, 2009). These features are diagnostic of the Ngandong sample yet do not appear in ancient or modern Australian groups that are claimed as their descendants by continuity advocates. Indeed, they have not been tested for in most projects that have examined the case for regional continuity in the area.

In light of these arguments, it is apt to discuss Webb's (2006) recent assertions that the "robust" early Australians may differ from the Ngandong people in particular details like browridge form or patterns of cranial thickening but that overall robusticity is still indicative of regional continuity. As he alleges, "taken in concert, the robust skeletal traits outlined above continue to point to an Indonesian origin, albeit most do not conform exactly to all the Javan traits" (Webb, 2006: 242). Webb (2006) proposes that the differences between the "robust" Willandrans and the Ngandong folk can be explained by drift, isolation, localized selection, and mutation operating on small populations, among other factors. This argument is difficult to accept, however, because generalized robusticity is not a particularly compelling argument for continuity in the absence of any more specific *regional* traits. As mentioned above, alternative explanations for the origin of robusticity in Australia are available that do not require the Ngandong fossils as ancestors (e.g., Brown, 1989; Bulbeck, 2001; Pardoe, 2006). In the absence of specific regional features that link Ngandong to the Willandrans (see Westaway and Groves, 2009), there is no compelling reason to retain the Ngandong (or Sangiran) fossils as ancestors to modern Australians. Indeed, as discussed above, there is abundant reason to remove the Ngandong fossils from the ancestry of any Aboriginal Australian.

Based on this evidence, it would seem that the hypothesis of an Indonesian component to the ancestry of the first Australians cannot be supported. There are no specific regional characteristics that demonstrate an unequivocal link between the Sangiran or Ngandong fossils and early Australians.

Notes on WLH 50

Following the broader discussion of the case for regional continuity in Australasia, it would be prudent to discuss one particular fossil and its role in these arguments a bit more specifically. Since its discovery in 1982, the WLH 50 skull has figured prominently in most discussions of modern human origins in Australia (e.g., Thorne, 1984; Thorne and Wolpoff, 1992; Webb, 1989, 2006; Frayer et al., 1993, 1994; Stringer, 1998; Hawks et al., 2000; Wolpoff et al., 2001). While the fossil is certainly interesting for a number of reasons, it can be argued that the

attention WLH 50 has received in the debate over modern human origins is disproportionate to the value that specimen has for illuminating any answers. Brown (1995: 27) rather colorfully referenced previous discussions of the fossil as “present[ing] the undated, poorly provenanced, probably pathological, and still undescribed Willandra Lakes 50 cranium as some Pleistocene equivalent of The Holy Grail.” While his statement is undoubtedly hyperbolic, it also contains more than a grain of truth. WLH 50 has never been properly described, is almost certainly pathological, and the dating of this specimen (Caddie et al., 1987; Simpson and Grün, 1998; Grün et al., 2011) has not supported previous suggestions that it is one of the more ancient human fossils in Australia (e.g., Flood, 1983; Habgood, 1986; Lahr, 1996). Yet, despite these shortcomings, WLH 50 is a prominent, and sometimes the sole (e.g., Frayer et al., 1993; Hawks et al., 2000; Wolpoff et al., 2001; Curnoe, 2009, 2011; Cartmill and Smith, 2009), fossil discussed as a key specimen in the Australasian fossil sequence. The attention that has been given this fossil skull deserves reevaluation for a number of reasons.

WLH 50 is an exceptionally massive skull, one of the most robust modern humans yet discovered. Its level of robusticity is unique even amongst the so-called “robust” early Australian groups like Kow Swamp. One of the more commonly discussed traits of WLH 50 is its cranial thickness (e.g., Brown, 1989; Stringer, 1992; Hawks et al., 2000), which reportedly exceeds the known Australian Aboriginal range (Brown, 1989). Figure 4.3 shows a simple plot of cranial thickness in a sample of Pleistocene/early Holocene Australians from Kow Swamp, Coobool Creek, Nacurrie, Mossgiel, Keilor, and the Willandra Lakes.

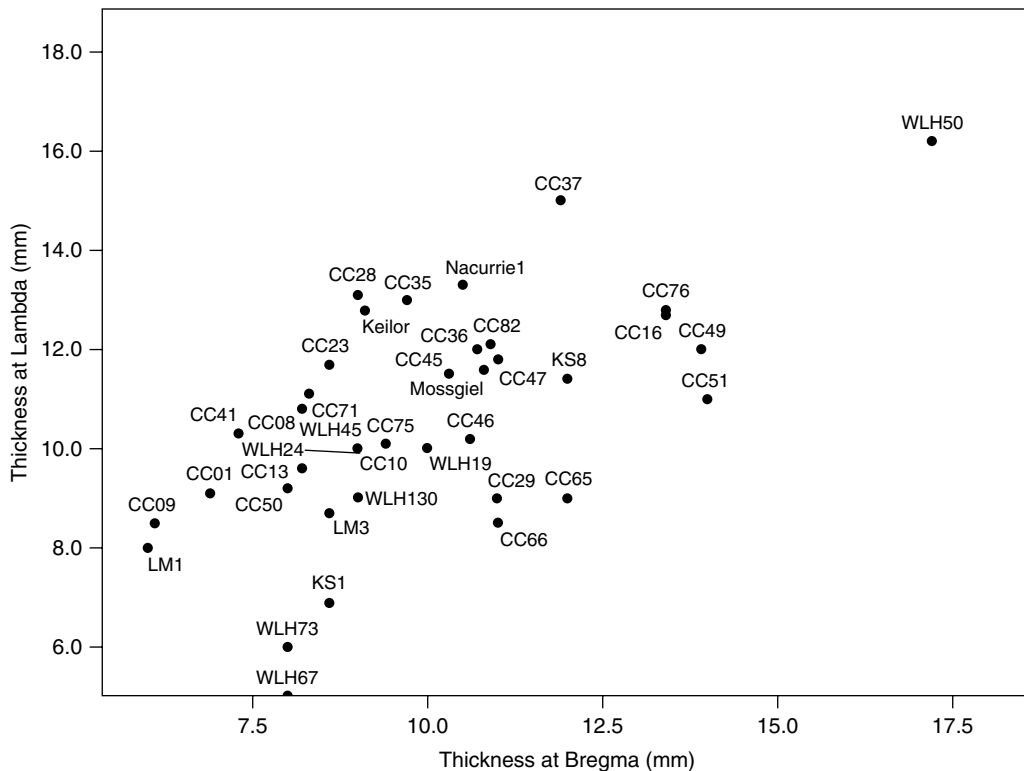


Figure 4.3. Cranial thickness at bregma and lambda in a sample of late Pleistocene and early Holocene Australian crania. Note the location of WLH 50 relative to its peers. Data provided by Webb (2006) and Peter Brown (<http://www-personal.une.edu.au/~pbrown3/resource.html>).

WLH 50 falls well outside the point cloud formed by its contemporaries, with a thickness at lambda that is 8% greater than the next largest measurement (Coobool Creek 37) and a thickness at bregma that is nearly 23% larger than the next closest measurement (Coobool Creek 51). While remarkable in the Australian Pleistocene sample, these measurements are not unusual for WLH 50, whose average cranial vault thickness is roughly 25% greater than the average for the rest of the Willandra Lakes sample (data provided in Webb, 2006: 194). While a very few of the Willandra Lakes crania may match or even slightly exceed the thickness of WLH 50 at inion (i.e., WLH 19, 27, and 28; data from Webb, 2006), it is clear that the overall pattern of vault thickening in WLH 50 is unique and exceptional.

The unusual size and dimensions of WLH 50 have also received attention, with both Wolpoff (1999) and Hawks and colleagues (2000) taking pains to portray WLH 50 as somehow falling within normal parameters of variability for late Pleistocene Australians. According to those authors, “some of the Australian crania dated the terminal Late Pleistocene or Holocene from Coobool (Creek), as well as others such as Cossack, *are as large as WLH-50*, or for some dimensions even larger” (Hawks et al., 2000: 15; italics in original). It is curious, however, that none of these other Australian crania mentioned, like Coobool Creek 5 and 76 or Cossack (Hawks et al., 2000), have ever received a similar level of attention from these authors in papers purporting to demonstrate regional continuity. If, indeed, there are many crania exhibiting such similar dimensions and characteristics, why focus so heavily on WLH 50 to the exclusion of other worthy examples?

Many workers attribute the unusual vault thickness and overall size in WLH 50 to an as-yet unnamed pathology. Webb (1989, 1990, 1995, 2006) has argued that the extreme thickness of the WLH 50 cranial vault is consistent with a hemolytic or metabolic disorder. This diagnosis is bolstered by the construction of the cranial vault in WLH 50, which is comprised almost solely of thicker diploë with only very thin inner and outer cranial tables (Webb, 1989, 2006; Westaway, 2006). Brown (1989: 70) disagrees with this diagnosis because the “uniformity with which this (thickening) occurs throughout the vault is not consistent with the osteological changes associated with (these) disorders” (though see Curnoe, 2011). Unfortunately, Brown (1989) did not suggest any alternative explanation. Paget’s disease has also been mentioned as a possible cause for this unusual thickening (Westaway and O’Neal, 2005) but has since been dismissed because the apparent sclerotic remodeling seen in CT scans is actually the result of diagenesis. Webb (2006: 198) has recently tried to temper his earlier (1989, 1990, 1995) arguments for pathological thickening in WLH 50, stating that “WLH 50 is a very robust individual with or without pathology, because other heavily developed features are clearly not pathological . . . this individual would have had a thick vault in keeping with its other robust features.” While this argument makes sense, it also highlights the difficulty in trying to understand what the morphology of WLH 50 means for our understanding of the ancient Australian record. What Webb (2006) and others have succeeded in demonstrating is just how unusual WLH 50 is in terms of its thickness and robusticity.

Lastly, the dating of WLH 50 would not support its position as a key transitional specimen in Australia. While the initial references to this fossil often refer to it as one of the earliest fossils in Australia (e.g., Flood, 1983; Habgood, 1986), more recent dating work has not borne out this claim. Being a surface find it has proven challenging to place this individual within the stratigraphy of the site, but since numerous remains from a single individual were located in the same vicinity, and there is minimal surface erosion to the bone, it is unlikely that significant transport of the remains occurred before their discovery. Dating of WLH 50 remains themselves has provided some context. Initial ESR dates done by Thorne suggested a date for WLH 50 of around 30 kyr (Clark, 1987). A later U-series date undertaken on bone provided an age of 29 kyr (Caddie et al., 1987). Gamma spectrometric U-series dating returned an age of only 14 kyr (Simpson and Grün, 1998). The most recent, and most comprehensive,

attempt to date WLH 50 places it between 12.2 and 32.8 kyr (Grün et al., 2011). As present evidence has humans occupying Australia conservatively at 45 kyr (e.g., O'Connell and Allen, 2004), and quite probably at 50 kyr (Bowler et al., 2003; though see Rasmussen et al., 2011, for possible evidence of earlier migrations), these ages suggest that WLH 50 dates to at least 13 kyr and possibly as much as 38 kyr after the arrival of the first Australians. This would place WLH 50 closer to the Last Glacial Maximum, which began about 30 kyr and ended around 15 kyr, and would instead suggest that the more securely dated Lake Mungo 1 and 3 individuals (e.g., Bowler et al., 2003) are most representative of the earliest Australians.

As WLH 50 is clearly unusual in its morphology, falls outside the normal range of variation for Pleistocene Australians, is likely pathological to some degree, and probably dates to at least 13 kyr after the initial colonization of Australia, it is perplexing that this individual has received this degree of notoriety in the debate over the origins of modern humans in Australia. One would be hard pressed to name another undescribed fossil that has achieved the level of attention and importance lavished upon WLH 50. Indeed, the perceived importance of this fossil well outweighs the actual contribution that this individual can make in elucidating the origins of Australians. While it is often highlighted for its unusual, extreme morphology, it is because of this singular anatomy that WLH 50 is arguably of less importance for our understanding of modern human origins than any other single specimen in Australia. With dozens of skeletons represented from that age (or older) and area of the continent, seeking to explain human origins in Australia in reference to WLH 50, while ignoring every other individual represented in that sample, is not an appropriate research design. To borrow and modify Pardoe's (2006) discussion on theoretical approaches in biological anthropology, we must move from a more paleontological focus on individual fossils as exemplars to a focus on the population with the Australian record. Were WLH 50 the only ancient Australian specimen known we could be forgiven for spending so much time analyzing its morphology. But WLH 50 is not alone, and it is clear that he represents the most extreme example among the dozens of individuals that have been recovered from the Willandra. A more productive approach would be to move away from focusing on the modern human sample from Australia as disparate individuals and try to see what they can tell us as a population. Examples of this type of approach have been provided by Brown (1989) and more recently by Westaway and Groves (2009).

Genetic Evidence for the Colonization of Australia

Genetic studies are sometimes difficult to conduct in Australia due to opposition by Aboriginal groups (e.g. van Holst Pellekaan, 2011), but many groups are becoming more interested in partnerships with evolutionary biologists. The molecular evidence collected to date has consistently identified Australia as an early destination for modern humans, providing independent support for similar conclusions derived through archaeology (e.g. Bowler et al., 2003; O'Connell and Allen, 2004; Hiscock, 2008). Y chromosome and mtDNA haplotypes provide support for migrations to Australia through South Asia that predate 50 kyr (Keinan et al., 2007; Gutenkunst et al., 2009; van Holst Pellekaan, 2011). Indeed, a recently sequenced complete genome provides evidence for the divergence of a human lineage at approximately 75 kyr that eventually reached Australia (Rasmussen et al., 2011). While previous work showed no evidence from living Australians for the survival of any archaic DNA material (Van Holst Pellekaan et al., 2006; Hudjashov et al., 2007), recent research in ancient DNA changed this picture significantly. We now know that both Neandertal and Denisovan DNA is present at low frequencies in Australians (Reich et al., 2011; Rasmussen et al., 2011). These data suggest that the earliest modern occupants of

Australasia assimilated genes from Eurasian archaic populations sometime during their eastward migration.

Work on ancient DNA from fossils purported to be representative of both “robust” and “gracile” Australians demonstrates that none of the sampled individuals lie outside of the range of modern Aboriginal genomic variation (Adcock et al., 2001a; Groves, 2001; Relethford, 2001a; Cameron and Groves, 2004: 271). Lake Mungo 3 is the notable exception in this work, although it has been suggested that contamination by nDNA inserts (numts) may have resulted in the observed mtDNA sequence (Colgan, 2001; Trueman, 2001; Groves and Cameron, 2004: 271–272). These latter papers suggest that Lake Mungo 3 is not representative of an earlier divergence but instead reflects modern contamination with nDNA that has created a pseudogene signature (Colgan, 2001; Trueman, 2001; Groves and Cameron, 2004: 271–272; though see Adcock et al., 2001b). Additionally, some questions have been raised about the likelihood of preservation of ancient DNA at Lake Mungo due to the thermal history at the site (Smith et al., 2003). As one of us (MCW) recently resampled the individuals sequenced by Adcock and colleagues (2001a), independent tests of the presence and significance of this ancient DNA will be forthcoming.

The “Hobbit”

The controversies generated by the *Homo floresiensis* sample from Liang Bua are also deserving of some comment here. While a lengthy treatment of these remains is beyond our purview for this chapter (see Aiello, 2010, for an excellent recent review), the perception that these remains could represent modern humans, albeit pathological ones, warrants some discussion.

First published in October 2004 (Brown et al., 2004), the Liang Bua remains were instantly the subject of both fascination and controversy. While that initial publication included only two individuals, the LB 1 skeleton and an isolated P₃ referred to as LB2, subsequent publications (e.g., Morwood et al., 2005, 2009) have expanded the sample to include as many as fourteen individuals. All of these individuals are short in stature, with LB 1 reconstructed to be ~106 cm in height (Brown et al., 2004) and the individual represented by the LB 8 tibia thought to be slightly shorter than that (Morwood et al., 2005). All of the published remains are fairly consistent in their small size, indicating that LB 1 is not unusual for this population in terms of stature or body proportions. LB 1 does have the only preserved skull, however, and this circumstance has provoked the most heated debate. The cranial capacity for this individual, initially estimated as 380 cm³ (Brown et al., 2004) and later revised upward to 417 cm³ (Falk et al., 2007), is among the lowest ever recorded for a hominid. This feature, more than any other characteristic of these remains, has driven the debates surrounding the “Hobbit.”

Several workers have been critical of the new species designation given to the Liang Bua fossils and prefer to explain the unusual stature and cranial capacity of LB 1 as the result of any number of pathologies operating on an otherwise modern human. These include microcephaly (e.g., Henneberg and Thorne, 2004; Jacob et al., 2006; Martin et al., 2006; Martin, 2007) as well as other conditions like Laron Syndrome (Hershkovitz et al., 2007, 2008), MOPD II (Rauch et al., 2008), or Myxoedematous Endemic Cretinism (Obendorf et al., 2008). These diagnoses of pathology have been shown to be problematic on several fronts. Falk and colleagues (2005, 2007, 2009a) have repeatedly demonstrated that the endocast of LB 1 does not exhibit signs of microcephaly and instead resembles *H. erectus* endocasts in some statistics and consistently groups with non-pathological modern humans in other aspects of brain shape (though see Weber et al., 2005 and Martin et al., 2006, for counter-arguments). Other developmental abnormalities discussed by Jacob and colleagues (2006) have been shown to

fall within the normal range of variation for humans or apes (Baab and McNulty, 2009; Larson et al., 2009; Kaifu et al., 2009; Jungers et al., 2009a; Aiello, 2010). The evidence for both Laron Syndrome and cretinism has likewise been dismissed (Brown and Maeda, 2009; Falk et al., 2009b; Jungers et al., 2009a, 2009b; Brown, 2012). While the falsification of these hypotheses of pathology does not remove the possibility that LB 1 could be pathological in some way, there has yet to be a convincing argument made for a pathology that can account for the total morphological package of *H. floresiensis* (Aiello, 2010). In particular, the primitive anatomy of the wrist (Tocheri et al., 2007), the limb proportions (Holliday and Franciscus, 2009), the pelvis (Jungers et al., 2009a), and the unusual anatomy and proportions of the feet (Jungers et al., 2009b) are difficult to reconcile with any known pathological conditions in humans. Unless some argument for pathology that can effectively explain all these anatomical traits can be supported, these remains are best kept within this new species.

At present, the evidence suggests that *H. floresiensis* may represent the descendents of pre-*erectus* hominids that had both smaller bodies and brains (e.g., Brown and Maeda, 2009). Argue and colleagues (2009) found two equally parsimonious cladograms that are supportive of this argument, placing *H. floresiensis* nearest to representatives of early *Homo*. While Zeitoun (2009) found that *H. floresiensis* grouped with *H. erectus*, he did not factor skull size into the characteristics used to generate his cladograms. Of course, the possibility that *H. floresiensis* simply represents a dwarfed version of *H. erectus* was the earliest hypothesis suggested by its descriptors (Brown et al., 2004), but that theory is now discounted by most workers (Aiello, 2010). It is hoped that future excavations on Flores or surrounding islands will yield fossils of these pre-*floresiensis* hominids.

The late survival of *H. floresiensis* has served to enliven the debate surrounding the route that modern humans may have taken to Australia. As modern humans were in southeast Australia by at least 43 kyr (e.g., Bowler et al., 2003), the possibility that those earliest migrants may have encountered *H. floresiensis* is intriguing. The so-called northern route would have taken modern humans to Australia via Borneo, Sulawesi, and New Guinea, a route that would have left *H. floresiensis* undiscovered by *H. sapiens*. Early dates from East Timor, however, suggest that the southern route of migration east from Java through Bali, Lombok, and Flores to Sahul may have been used (e.g., O'Connor, 2007). There could have been multiple routes to bring early inhabitants to East Timor (e.g., Aiello, 2010), so this question will remain unsettled pending further work in the region.

This evidence suggests that *H. floresiensis* presents an interesting but somewhat tangential case for the origins of the modern inhabitants of Australasia. While this species appears to have been evolving alongside modern inhabitants of island Southeast Asia and Australia, we feel that the evidence does not support the contention that these remains represent a pathological or abnormal modern human population.

Discussion

The debate over MHO in Southeast Asia and Australia has a long and storied history. The discoveries at Talgai and Trinil began a discussion that shows no signs of ending any time soon. Throughout much of this debate, Australasia has been depicted as an example of various types of regional continuity, whether those genetic contributions came from three founding populations (Birdsell, 1949, 1967) or two (Thorne, 1971, 1980; Webb, 2006). These migration models explain variation in early modern Australians through amalgamations of different types of people and argue that either anthropometric measurements of living people (e.g., Birdsell, 1949, 1967) or skeletal remains left behind in the archaeological record (e.g., Thorne, 1971; Webb, 2006) provide evidence for these discrete migrations. These ideas

have been very influential and have framed the discussion over human origins in this part of the world. As more evidence has been uncovered, however, and as that evidence has been further scrutinized, it is clear that the evidence for multiple founding populations for Australia is simply not supported by the data. As Larnach (1974: 213) found, “images of Negritos, Murrayians, and Carpentarians are ghost images which disappear as we trace them back towards Aboriginal beginnings,” and much the same can be said for separate groups of “robust” and “gracile” early Australians.

What the evidence does show us is that the earliest Australians were indeed modern humans (e.g. Wolpoff, 1999), and that these earliest inhabitants do not exhibit any evidence for specific Australasian regional traits that would indicate in situ evolution of that modern form (e.g. Thorne, 1971, 1980; Thorne and Wolpoff, 1981; Wolpoff et al., 1984; Wolpoff, 1999; Webb, 2006) nor the assimilation of genes from Indonesian *H. erectus* (or *H. soloensis*) into their gene pool (e.g. Smith et al., 1989; Smith, 1992, 2010). While small groups of fossils (e.g. Thorne, 1971, 1976, 1980; Thorne and Macumber, 1972; Wolpoff et al., 1984; Wolpoff, 1999; Curnoe, 2007) or individual crania (e.g. Frayer et al., 1993; Hawks et al., 2000; Wolpoff et al., 2001) have been highlighted for the perception that these individuals retained characteristics that belied a link to regional archaic groups, these ideas are no longer defensible. On the other hand, acceptance of a traditional single-origin replacement model for the origins of Australian Aboriginals is difficult in light of the recent advances in our understanding of the human nuclear genome. The presence of both Neandertal and Denisovan nuclear DNA in Australian samples (e.g. Rasmussen et al., 2011) suggests that the ancestors of modern *H. sapiens* were interbreeding with archaic hominids in at least some parts of the world. Because the genetic contributions made by Neandertals are generally consistent among different regional populations of modern humans, it is likely that this interbreeding happened relatively early in our population expansion across the Old World. The more varied distribution of Denisovan DNA in regional modern groups may indicate a more localized, and complex, dispersal of those genes. Together, the fossil and genetic evidence appear to be most compatible with an Assimilation model of MHO, combined with the localized extinction of archaic hominids like Ngandong. This scenario reflects Relethford's (2001: 206) contention that “[l]ocal populations frequently became extinct and were replaced by migrants from neighboring populations....” A traditional replacement model would predict that the Ngandong hominids would be supplanted by hominids with a purely African origin, but this is not consistent with recent genetic data. The Ngandong hominids went extinct and were indeed replaced, but the subsequent migration of modern humans into Australasia carried genes acquired through admixture with archaic populations prior to their arrival in this region.

Instead, the disappearance of regional archaic groups like the hominids from Sangiran, Ngandong and Flores and subsequent replacement of those groups by an influx of modern humans to the area is best supported by the present data. Recent work on the dating of the Ngandong fossils (Indriati et al., 2010, 2011) suggests that previously accepted recent dates for these individuals (e.g., Swisher et al., 1996, 1997) can no longer be supported. The new dates of between 143 and 546 kyr for Ngandong (Indriati et al., 2011) accord well with the paleoecological scenario prepared by Storm (2000, 2001a, 2001b), which posits the disappearance of the population sampled at Ngandong during a faunal turnover on Java that took place about 126 kyr. As there is no evidence of modern humans on Java until the Punung (e.g., de Vos, 1985), or, more firmly, into the Holocene (Storm, 1995; Shutler et al., 2004), it does not appear that those modern humans would have had the opportunity to interact with the population represented by the Ngandong fossils. While Webb (2006) has suggested a possible migration of *H. soloensis* to Australia as early as 160 kyr, there is currently no archaeological or skeletal evidence to support this position.

As argued elsewhere (e.g., Zeitoun, 2002; Widiyanto and Zeitoun, 2003; Durband, 2004, 2007, 2008c; Kaifu et al., 2008), the fossils from Ngandong, Sambungmacan, and Ngawi show considerable morphological differentiation from earlier Indonesian fossils from Sangiran and elsewhere and are not derived in the direction of modern humans. The appearance of numerous traits that are apparently autapomorphic in the Ngandong series (including Sambungmacan and Ngawi) is suggestive of considerable genetic drift in an isolated relict population. The fossils of *H. floresiensis* are likewise indicative of a localized and unique pattern of evolution occurring in isolation (e.g., Morwood and Jungers, 2009). During the Pleistocene Java was only intermittently connected with the mainland (Aziz et al., 1995), and the Ngandong fauna shows signs of endemism (van den Bergh, 1999; van den Bergh et al., 2001). Even when connected to the mainland, greater Sunda would have been at the peripheries of the known range of *H. erectus*, and its inhabitants would have formed an essentially allopatric population. In these conditions, the further evolution of *H. erectus* into new species like *H. soloensis*, and the evolution of *H. floresiensis* from some as yet unidentified source, would not be unexpected.

While much has been accomplished in our search to uncover the origins of modern humans in Australasia, obviously even more remains to be learned. Alan Thorne's paleo-anthropological contributions to this endeavor are well known, but his efforts to engage the Aboriginal communities impacted by his research have not been as well publicized. His work to form positive relationships with the Aboriginal groups in the Willandra has served as a model for responsible scientists to follow. The return of the woman known to science as Lake Mungo 1 to the Aboriginal community served as a rapprochement between scientists and Indigenous Australians. These efforts have paid considerable dividends in our ability to continue scientific work on those remains and lead us to be optimistic for the future of paleoanthropological work in this fascinating area.

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Chapter 5

Modern Human Origins in Central Europe

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Introduction and a Short Historical Background

The review of Central European late Pleistocene fossil hominins included in the 1984 Smith and Spencer volume began with a 1905 quote from Marcellin Boule lamenting the limited availability of information on human remains from Central Europe to Western European (particularly French) scholars (Smith, 1984). The availability of information and the use of Central European information certainly improved between 1905 and 1984. In 1906, for example, Dragutin Gorjanović-Kramberger published his exhaustive monograph on the Neandertal remains from Krapina, the first truly comprehensive monograph on Neandertals, and Gustav Schwalbe (1906) made extensive use of Central European specimens in his treatise on the “Prehistory of Man.” Similarly, Aleš Hrdlička (1915, 1930) provided significant coverage of Central European materials in his assessments of the human fossil record. Still, Boule and Vallois’s 1957 version of *Fossil Men* provides a far more detailed perspective on Western than Central European hominins and includes almost no coverage of the interpretation of human evolution given by researchers like Schwalbe and Gorjanović-Kramberger, who based their interpretations more on the Central European record.

By 1984, this had certainly changed, due in no small part to a review of Central Europe by Jan Jelinek in 1969 and the impact of the Vindija Neandertal sample (Malez et al., 1980; Wolpoff, 1980; Wolpoff et al., 1981). Beginning with the mid-1980s, the Central European fossil record played a significant role in explanations of modern human origins in Europe and beyond (cf. Smith, 1982, 1984). No longer did the Western European record hold complete sway in such discussions as it had essentially since the late nineteenth century and particularly since the publication of Boule’s (1911–1913) classic monograph on the La Chapelle-aux-Saints Neandertal partial skeleton. Furthermore, the Central European fossil record was crucial in dismantling the classic pre-sapiens argument, as the fossils from this region seemed to offer evidence of regional evolutionary continuity from pre-Neandertals through Neandertals to modern humans (Brace, 1964; Jelinek, 1969; Wolpoff, 1980).

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Although improved from earlier times, the chronology of the Paleolithic and hominin fossil records by the 1980s was still sufficiently loose so that gradual, in situ, continuity (Smith, 1984; Wolpoff et al., 1984) was a feasible explanation of the relationship between Neandertals and early modern humans in Central Europe. In large part this was due to the fact that a strong case could be made at this time that modern humans appeared essentially contemporaneously in the Old World, and thus that a classical multiregional pattern of modern human origins was eminently defensible (Smith, 1985). The Krapina-Vindija sequence from Croatia was central to this interpretation, but other fossils were ordered into it, as well. Like the Vindija fossils, the Šal'a frontal was interpreted as more modern-like than other Neandertals and was posited as a relatively late one (Vlček, 1969; Smith, 1984). The “well-dated” “36 ka” Hanhöfersand and “34 ka” Velika Pečina frontals were interpreted as transitional (Smith, 1984) between Neandertals and later modern Europeans, or at least as evidence of admixture between Neandertals and modern humans (Bräuer, 1984, 1989).

Since 1984, many more things have changed. Stringer and Andrews, in their 1988 *Science* paper, synthesized new genetic research¹ with the fossil record and argued that there had been no regional continuity in Eurasia across the archaic-modern boundary. Neandertals had become extinct without issue, they argued, which meant that the Central European fossil record had been misinterpreted as evidence of such continuity. The application of new chronometric techniques, particularly electron spin resonance (ESR), thermoluminescence (TL), and accelerator mass spectrometry (AMS) radiocarbon, to critical sites and specimens increasingly demonstrated that modern humans appeared early in Africa, slightly later in the Near East, and relatively late in Europe—including Central Europe (see review in Klein, 2009). This same chronology showed that Neandertals also survived at least a few millennia after moderns arrived in Central Europe (Churchill and Smith, 2000). The aforementioned genetic evidence was based on interpretations of mitochondrial DNA variation in extant peoples, but this interpretation was soon supported by other studies of both mitochondrial and somatic nuclear DNA, as well as Y chromosome analyses (cf. Underhill et al., 1997; Thomson et al., 2000). Perhaps even more influential has been the recovery of both mitochondrial and nuclear DNA from Neandertals and the former from a few European Upper Paleolithic specimens.² Although there were some cautionary voices (e.g., Relethford, 2001a; Templeton, 1993, 2005; Serre et al., 2004), the seemingly majority view from 1990 through 2010 was that genetic data both demonstrated a species-level difference between Neandertals and modern humans and denied any ancestral role for the former in the latter. Bolstered by the genetic studies, morphological arguments became increasingly more focused toward asserting the lack of any anatomical evidence of Neandertal–early modern human introgression. The combined effect of the genetic, chronological, and morphological studies is perhaps best exemplified by the 2009 statement that it is these “fresh data” that “have eliminated all reasonable doubt in the century-old controversy over the fate of the Neanderthals” (Klein, 2009: 751).

Specifically for Central Europe, an improved overall chronological perspective has helped to clarify many aspects of later human evolution. For example, direct dating of some specimens that were considered representatives of the earliest modern people in Central Europe (Table 5.1) has demonstrated each to be latest Pleistocene or more recent in age, and critical sites and specimens now have reliable age estimates.³ Significant fossil samples have entered the discussion, particularly the Peștera cu Oase and Muierii material from Romania (Dobos et al., 2010; Soficaru et al., 2006; Trinkaus et al., 2003a, 2003b, 2006b) and the Mala Balanica specimen from Serbia (Roksandic et al., 2011). Also, additional discoveries have been made at Dolní Věstonice in the Czech Republic (Sládek et al., 2000), and the entire sample has undergone major reanalysis (Trinkaus and Svoboda, 2006). A complete reanalysis of the Mladeč sample, also from the Czech Republic (Teschler-Nicola, 2006), and new analyses on the Krapina Neandertals (Monge et al., 2008) have been published. While all of these studies are important

Table 5.1. Revised dating for presumed early modern human fossils from Central Europe.

Specimen	Supposed Date			Revised Date		
	¹⁴ C age or association	Lab No.	Reference	¹⁴ C age or period	Lab No.	Reference
Western						
Binshof	21,300±320	Fra-40	Henke, 1980	3,090±45	OxA-9880	Terberger & Street, 2001
Hahnöfersand	36,300±600	Fra-24	Bräuer, 1980	7,500±55	OxA-10306	Terberger et al., 2001
Keisterbach	31,200±600	Fra-?	Protsch & Semmel, 1978	Specimen missing, cannot be redated		Street et al., 2006
Paderborn-Sande	27,400±600	Fra-15	Henke & Protsch, 1978	238±39	OxA-9879	Street & Terberger, 2002
Vogelherd	30,162±1,340	H 4054-3210	Conard & Bolus, 2003	3,980±30 to 4,995±35	KIA 19537 KIA 19540	Conard et al., 2004
Eastern						
Balla	22,300±180 20,000±190	GrN-4660 GrN-4661	Vögel & Walterbolk, 1972	6,660±50	GrA-24712	Tillier et al., 2009
Krems-Hundssteig	Gravettian?		Jungwirth & Strouhal, 1972	3,540±35 3,480±35	OxA-8291 OxA-8290	Trinkaus & Pettitt, 2000
Podbaba	Aurignacian?		Matiegka, 1924	Fossil destroyed, 1921		Churchill & Smith, 2000
Svitávka	Aurgnacian?		Klíma, 1963	1,180±50	GrA-13711	Svoboda et al., 2002
Velika Pečina	> 33,850±520	GrN-4979	Vögel & Walterbolk, 1972	5,045±40	OxA-8294	Smith et al., 1999
Zlatý Kůn	Aurignacian?		Prošek et al., 1952	12,870±70	GrA-13696	Svoboda et al., 2002

in their own right, they underscore what is truly the most significant change that has impacted the study of late human evolution in Central Europe. Prior to the reunification of Germany and the subsequent collapse of the Iron Curtain, access to much of the pertinent Central European record was limited. Communication was often challenging, and permission to study many sites and samples was difficult to come by and often quite restricted. This is generally no longer the case. There has been a marked increase in cooperative studies by researchers from many countries on this material. From our perspective, the increased emphasis on the Central European role in modern human origins derives from this more extensive interaction between researchers and the more open access to some material today as compared to 1984.

The following review comments further on these issues and endeavors to bring the most recent perspectives on this critical region into a clearer focus than was possible in 1984. It is not our intention to repeat the morphological details presented in the previous review (Smith, 1984) unless there have been significant changes. As in 1984, the information presented here is divided by affinity (Neandertal or modern). Geographical coverage mirrors that in 1984, except that the division is western and eastern rather than northern and southern. The eastern region consists of the Pannonian Basin, the surrounding highlands that define the basin, and areas adjacent to the highlands but not in the basin itself (Figure 5.1). The highlands form two crescent-shaped systems, one extending from the Alps southward as the Dinaric Alps (Dinarides) along the Adriatic. Toward the south the mountains extend eastward through to the Black Sea and are essentially contiguous with the mountains of Greece to the south. The western crescent is much more rugged and imposing than the eastern crescent, which extends much more intermittently first to the east and then to the south. This eastern crescent is formed by the Transylvanian Alps, Carpathians, Tatra, Sudetes, Erz, and the Bohemian and Bavarian highlands.

Most of the eastern region sites are associated with drainage systems that extend into the highland regions surrounding the Pannonian Basin, but some are located either further into the basin itself, on the opposite side of the highlands from the basin, or in highlands technically not forming the Pannonian Basin. The best examples of the latter are the early modern human sites of Cioclovina, Muierii, and Oase in Romania. These sites are located in areas surrounding the broad Wallachian Plain that marks the Danube's flow toward the Black Sea. Sites like Mujina Pećina on the western slopes of the Dinaric Alps and others on the Adriatic Coast (Karavanić and Smith, 2011) have not yielded human fossils⁴ but show that these areas were occupied during the late Pleistocene as well.

Western Central Europe is less precisely defined by geography. Here, we define it as the territory lying north of the highlands described above, extending to the North and Baltic Seas, and essentially from east to west between the Oder and the Rhine River drainages. This is essentially the German portion of the North European Plain. To some degree the separation of this plain from areas to the southwest and east is somewhat arbitrary. Also, relatively moderate highland areas separate this region from eastern Central Europe, and these are penetrated by several river systems, notably the Elbe (Labe) and Danube (Donau). Additionally, ice-free corridors likely linked them throughout the later Pleistocene (Kukla, 1978). Thus, the eastern and western regions of Central Europe were connected throughout the period of interest here, and human populations from the regions were most likely in rather close contact.

Conard and Bolus (2003; Conard, 2006) have focused on the Danube as a major artery for the spread of modern people and their cultural manifestations into Europe. While fossil evidence is non-existent currently (Conard et al., 2004), the early dates for the Aurignacian in the Swabian Jura⁵ indicate that modern people may well have used the "Danube Corridor" to enter Europe. However, as discussed later in this review, more evidence is needed to assess this specific issue. Regardless, the Danube River valley was undoubtedly a major artery for movement into and through both regions of Central Europe.



Figure 5.1. Physical map of Central Europe. The dotted line demarcates the western and eastern regions of Central Europe as used in this chapter. Map made with ESRI ArcMap v.10. The basemap is the U.S. National Park Service Natural Earth physical map.

Much of this chapter comprises an overview of the Central European Late Pleistocene hominin fossil record. This overview begins with the Neandertal remains followed by the early modern human remains. Post-Gravettian human remains are, for the most part, not discussed, as our attention is on the pattern and process of Neandertal and early modern human evolution. Following the discussion of the fossil record, we endeavor to provide a critical analysis of the fossil record and the theoretical perspectives that have been applied to its interpretation. Specifically, we bring the Central European fossil record to bear on the following issues: (1) the problem of typology in understanding biology and culture across the transition, (2) the pattern of biological variation among Neandertals, (3) the appearance of modern humans and the disappearance of the last Neandertals, and (4) the degree and pattern of Neandertal and early modern human admixture. The chapter ends with what we consider to be the best interpretation of the current evidence as well as a discussion of the limitations of this evidence.

The Central European Neandertal Fossil Record

The Central European fossil record has clearly been important for our understanding of European Neandertals. In addition to the Feldhofer discovery in 1856, other nineteenth-century discoveries in Central Europe (Šipka, Krapina) were important for demonstrating the validity of Neandertals as a prehistoric hominin population (Trinkaus and Shipman, 1992). Nevertheless, by the mid-twentieth century, the more numerous and better preserved Neandertal fossils of Western Europe had helped shift focus away from Central Europe.

Today, the Central European Neandertal fossil record (see Table 5.2 and Figures 5.2 and 5.3) remains sparse relative to that of Western Europe. Furthermore, aside from the Feldhofer 1 individual, the Neandertal remains are largely fragmentary, even if such sites as Krapina and Vindija preserve many individuals. Despite the limitations of this record, it is essential for understanding the process and dynamics of the origin of modern humans.

Neandertal Fossils from Western Central Europe

Over the last few decades, the fossil record of Neandertals from western Central Europe has only grown marginally beyond the important Kleine Feldhofer Grotte (Neandertal) and Ehringsdorf (see Smith, 1984) collections. Perhaps the most significant recent discoveries have come from the former, with over sixty new skeletal fragments discovered during 1997 and 2000 excavations of discarded cave fill from the original 1856 discovery (Schmitz et al., 2002). More discoveries have come in the form of fragments and/or isolated teeth.⁶

Ehringsdorf

Although Vlček (1993) argued that the Ehringsdorf specimens were more advanced in many ways than Neandertals, the overall morphology of the cranial remains, including the H skull and the mandibles, and postcranial remains is demonstrably Neandertal-like. Henke and Rothe (1994) and Street and colleagues (2006) also suggest that the Ehringsdorf sample exhibits weak development of Neandertal features, but this argument is countered by the specific Neandertal features of the cranium (suprainiac fossa, occipital bunning), the similarity of the two mandibles to other early Neandertals (e.g., Krapina) and the form of the femur (Cartmill and Smith, 2009; Smith, 1984). An OIS stage 7 age for the Ehringsdorf sample is commensurate with all of the age indicators, including chronometric dating of the travertines to ≥ 200 ka (Street et al., 2006).

Table 5.2. Neandertal fossil remains from Central Europe.

Site	Human Remains	Cultural Association	Date(s)	Date Reference(s)
Western Central Europe¹				
Hohlenstein-Stadel	Femur diaphysis	Mousterian	OIS 5, \approx 70–120 ka	Kunter & Wahl, 1992
Hunus	Right mandibular molar	Mousterian	Würm, < 76–79 ka	Rosendahl et al., 2006, 2011
Klausenhöhle-Klausennische	di, [†]	Mousterian	Ca. 50 ka	Schoch, 1973; Street et al., 2006
Klausenhöhle-Untere Klausse	Scapula (acromial end)	No provenience	No provenience	Schoch, 1973; Street et al., 2006
Kleine Feldhofer Grotte (Neandertal)	Partial skeleton and fragmentary remains of multiple individuals	Mousterian (Micoquian)	38.6–41.1 ka*	Schmitz et al., 2002
Ochtendung	Frontal & anterior parietals	Mousterian	OIS 6	von Berg et al., 2000
Salzgitter-Lebenstedt	Occipital & parietal	Mousterian	Weichselian 55.6 \pm 0.9 kyr BP ²	Hublin, 1984
Sarstedt, Haldesheim	Temporal, occipital & parietal	Mousterian?	Weichselian or Eemian	Czarnetzki et al., 2001
Sesselfelsgrötze	Two deciduous teeth, neonatal or fetal postcrania	Mousterian	M tooth: 61–91 ka (TL) G tooth & postcrania: 46–61 ka (TL & ¹⁴ C)	Rathgeber, 2003; Richter, 2002
Taubach	Left M ₁ , left dm ₁	“Proto-Mousterian” (Tayacian)	OIS 5e?	Behm-Blancke, 1960
Warendorf-Neuwarendorf	Parietal fragment	Mousterian?	\approx 50–70 ka ²	Czarnetski & Trelliso-Carreño, 1999; Street et al., 2006
Weimar-Ehringsdorf	Partial cranial, mandibular, and postcranial remains from at least nine individuals	Mousterian	\approx 230 ka	Blackwell & Schwarcz, 1986
Zeeland Ridges (North Sea)	Frontal bone fragment	None	Pleistocene	Hublin et al., 2009
Eastern Central Europe				
Crvena Stijena (Montenegro)	Canine ³	Mousterian? ²	> 39.3 ka ²	Morley & Woodward, 2011
Gánovce (Czech Rep.)	Partial cranial remains, endocast & molds of radius & fibula	Mousterian	OIS 5e	Višek et al., 1958
Krapina (Croatia)	Numerous remains of at least eighty-nine individuals	Mousterian	130 \pm 10 kyr BP (ESR)	Rink et al., 1995

(Continued)

Table 5.2. (Continued)

Site	Human Remains	Cultural Association	Date(s)	Date Reference(s)
Kůlna (Czech Rep.)	Maxilla	Mousterian (Micoquian)	45.7 + 2.9/- 2.2 kyr BP ²	Mook, 1988
Mala Balanica, Sićevo Gorge (Serbia)	Partial mandible ³	None	> 397–525 ka BP (US-ESR)	Rink et al., 2013
Ochoz-Švédův stůl (Czech Rep.)	Mandible, right M ₃ , parietal, temporal	1905: none 1964: Mousterian		
Ohaba-Ponor 1 (Romania)	Pedal phalange	Mousterian (with UP elements)	Early Würm	
Šal'a (Slovakia)	S1: frontal bone S2: parietal & partial frontal	None	OIS 5e	Sládek et al., 2002
Šipka (Czech Rep.)	Mandibular symphysis	Mousterian	OIS 3?	Kukla, 1954; Gábori, 1976; Smith, 1984
Stajnia (Poland)	Three teeth	Mousterian (Micoquian)	OIS 5c or 5a	Urbanowski et al., 2010
Suba-lyuk (Hungary)	Mandible, postcrania, partial child cranium	Mousterian (La Quina)	OIS 4 ²	Ringer, 1993
Vindija-level G ₃ (Croatia)	Numerous fragmentary remains	Mousterian	≈38–45.6 ka 38.3 ± 2.1 ky BP* > 42 ky BP*	Ahern et al., 2004; Krings et al., 2000; Serre et al., 2004

¹ Some or all of the fossils are known to be missing or destroyed.

* Direct date(s) on human remains.

¹ All sites are in Germany unless otherwise noted.

² Date is very tentative or problematic and should be regarded with caution.

³ Neandertal designation is unclear.

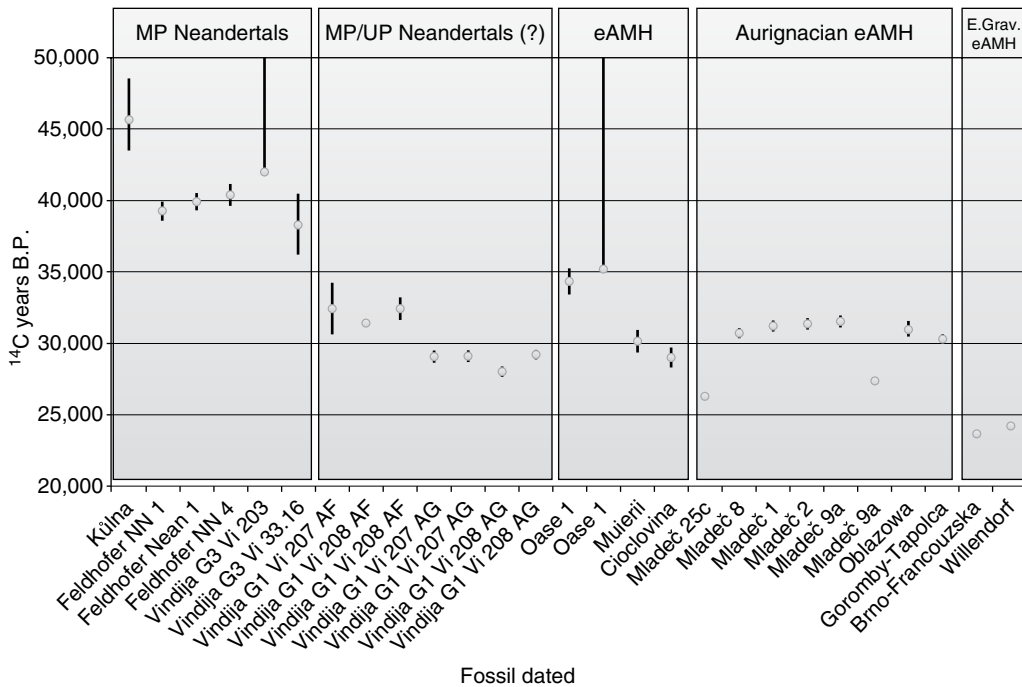


Figure 5.2. Direct radiocarbon dates of Central European Middle and early Upper Paleolithic fossils. “MP/UP Neandertals (?)” refers to fossils associated with the Szeletian *sensu lato*. The older dates for the Vindija level G₁ specimens (denoted by “AF”) are ultrafiltration AMS ones. Note: This graph does not include the direct AMS date for D.V. 35 (Trinkaus et al., 1999), since its young age, relative to the archaeological deposits at D.V. I, is likely due to contamination (Pettitt & Trinkaus, 2000).

Kleine Feldhofer Grotte

The location of the discarded sediments from the Kleine Feldhofer Grotte work in 1856 was discovered in 1997 during excavations led by R. Schmitz and J. Thissen. Work in this year uncovered twenty-four fragments of human bone, including a piece that fits onto the original Feldhofer 1’s left femur (Schmitz et al., 2002; Schmitz and Thissen, 2000). Artifacts were found that are attributed to both the Micoquian (late Middle Paleolithic) and the Gravettian. An additional thirty-four human specimens were found during renewed excavations in 2000. Aside from the femoral fragment, two other pieces, a left zygomatic-maxilla piece (NN 34) and piece of right temporal bone (NN 35), articulate with the original Feldhofer’s remains (Figure 5.4). Additional craniodental and postcranial remains discovered may also belong to the Feldhofer 1 individual, since they do not replicate any of the 1856 specimen’s preserved elements. Particularly informative are a chinless mandibular symphyseal fragment (NN 52), two large and heavily worn maxillary incisors (along with several other teeth), several hand bones—including a polical metacarpal with a characteristic flange for the *opponens pollicis* muscle, several vertebrae, and numerous other postcranial remains (Smith et al., 2006). However, some of the new fossils must have come from at least one other adult individual known on the basis of a second right humerus, a second right ulna, and other fragments, and possibly one subadult, represented only by a worn deciduous molar (Schmitz et al., 2002; Smith et al., 2006, 2008).

Although the presence of Gravettian artifacts in the cave fill elicits the possibility that some of the human remains could be modern humans, all of the diagnostic

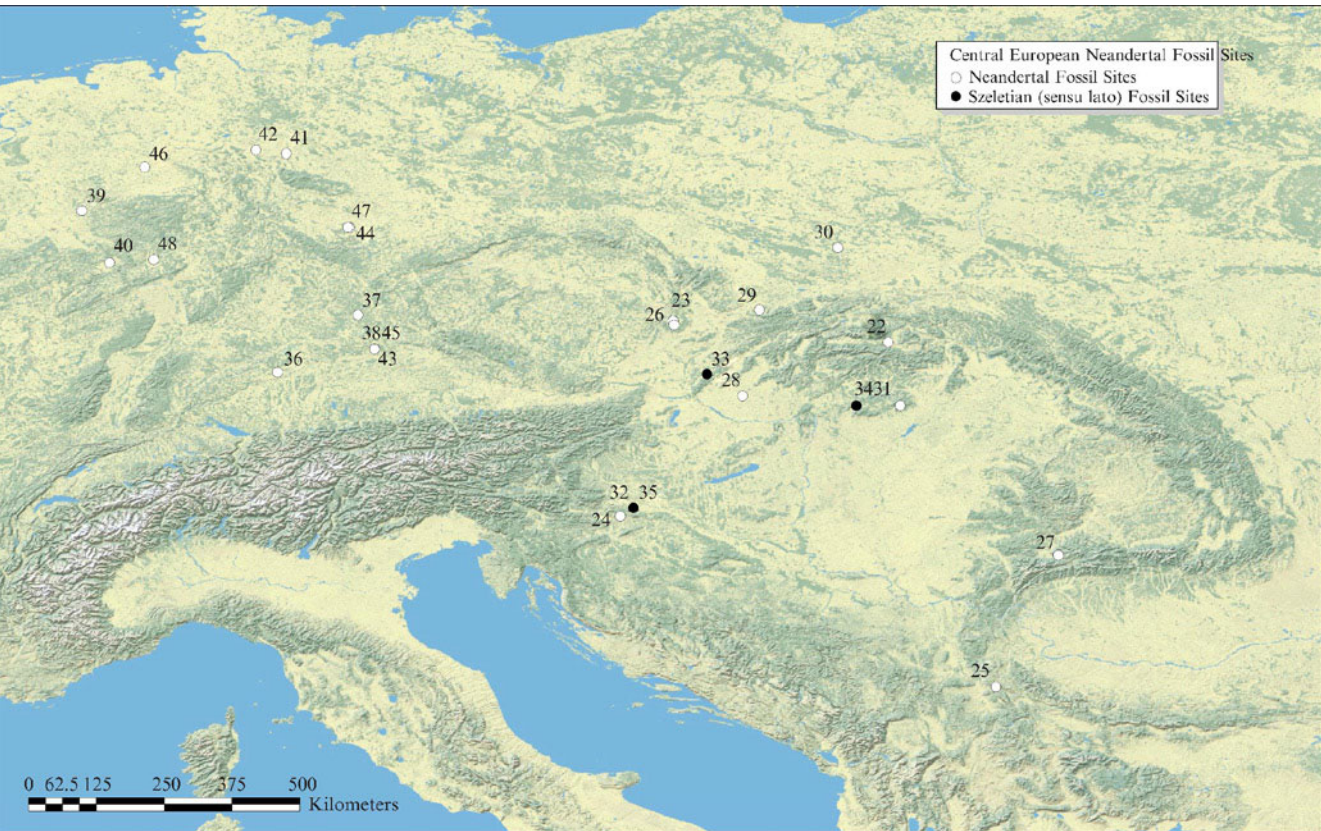


Figure 5.3. Map of Central European Neandertal fossil sites. Map made with ESRI ArcMap v.10. The basemap is the U.S. National Park Service Natural Earth physical map. Neandertal fossil sites: * 22: Gánovce; 23: Kůlna; 24: Krapina; 26: Ochoz (Švédův stůl); 27: Ohaba-Ponor; 28: Šal'a; 29: Šipka; 30: Stajnia; 31: Subalyuk; 32: Vindija G3; 36: Hohlenstein-Stadel; 37: Hunas; 38: Klausennische-Klausenhöhle; 39: Kleine Feldhofer Grotte (Neandertal); 40: Ochtendung; 41: Salzgitter-Lebenstedt; 42: Sarstedt; 43: Sesselfelsgrötte; 44: Taubach; 45: Untere Klause-Klausenhöhle; 46: Warendorf-Neuwarendorf; 47: Weimar-Ehringsdorf. Szeletian *sensu lato* (Neandertal?) fossil sites: 33: Dzeravá Skála; 34: Remete Felső; 35: Vindija G1. *Zeeland Ridges does not appear on this map. It is located in the North Sea at 51°40' N, 3°20' E. Crvena Stijena also is not plotted, since questions remain about its reported Neandertal affinities and its antiquity.

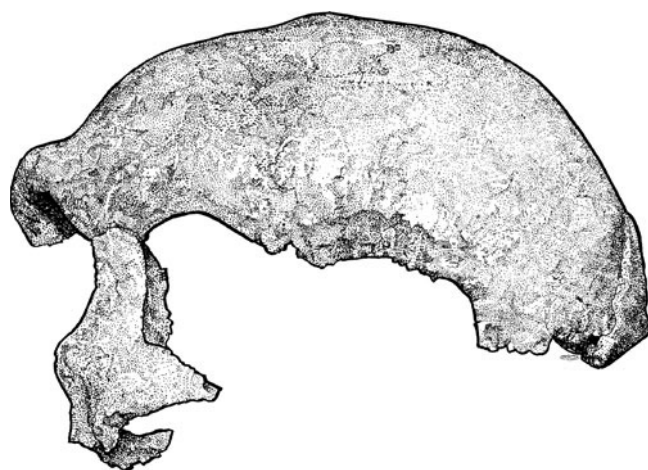


Figure 5.4. The left zygomatic-maxilla (NN 34) articulated with the Feldhofer 1 calotte. Illustration by M. Cartmill.

skeletal specimens are morphologically aligned with Neandertals. Additionally, a three-dimensional analysis indicates that the skeletal remains and Micoquian artifacts can be separated from the Upper Paleolithic tools (Feine, 2006). Stable isotopic studies of the Neandertal skeletal remains reveal a diet strongly focused on meat, but not fish (Richards and Schmitz, 2008), which is commensurate with Neandertal dietary results at other sites (Bocherens, 2011).

The NN 34 zygomatic-maxilla piece is perhaps the most informative of the new discoveries from Kl. Feldhofer Grotte. All of its anatomy is clearly Neandertal (e.g., multiple zygomaticofacial foramina, a columnar lateral orbital pillar, an oblique inferior zygomaxillary margin, and an enlarged maxillary sinus), and this further highlights the “classic” Neandertal appearance of the Feldhofer individual. Under previous interpretations (e.g., Smith, 1984) of the Feldhofer individual, the “classic” Neandertal gestalt was argued to be consistent with it not being a late Neandertal such as those found at Kůlna and Vindija. However, recent AMS ^{14}C dating of both the original Feldhofer 1 as well as two of the recently discovered specimens place the Feldhofer sample as very late. The dates range from $39.24 \pm 0.67 \text{ ka } ^{14}\text{C BP}$ for NN1 to $40.36 \pm 0.76 \text{ ka } ^{14}\text{C BP}$ for NN4, with Feldhofer 1 falling in between (Schmitz et al., 2002). The only Central European Neandertals that are directly dated and more recent are the potentially Upper Paleolithic-associated ones from Vindija G₁, while the Vindija G₃ Mousterian-associated fossils are approximately contemporary to the Feldhofer ones. This new chronological information demonstrates late survival for “classic” Neandertal morphology in Central Europe and contrasts with the “progressive” appearance of the Vindija remains.

In addition to the new fossil discoveries from Feldhofer, work in the 1990s also resulted in the first sequencing of Neandertal DNA extracted from the Feldhofer 1 humerus (Krings et al., 1997). For the 357 bp of mtDNA that was sequenced, the Feldhofer 1 individual fell outside the observed range for paired differences among living humans (although still within the range of probability) and suggested a Middle Pleistocene date of divergence between Neandertal and modern human mtDNA (Krings et al., 1997, 1999). Although much about Neandertal genetics has been learned since (Green et al., 2006, 2010; Hawks, this volume; Krause et al., 2010; Noonan et al., 2006; Schmitz et al., 2002; Serre et al., 2004), the original Feldhofer 1 sequencing was a breakthrough.

Zeeland Ridges

In 2001, the first Neandertal from the Netherlands was recovered off the Zeeland coast in the North Sea (Hublin et al., 2009). This area, known as the Zeeland Ridges, is a part of a large area called “Doggerland.” Though now submerged, this relatively shallow region was a part of the European mainland during much of the Pleistocene and earlier, and it has yielded extensive Pleistocene mammal collections over the years. Because of the circumstances, there are some questions regarding the exact age and context of the specimen (Hublin et al., 2009). Morphologically, however, it is a Neandertal frontal bone fragment from the left side that preserves a segment of the supraorbital torus and the squama above it. The torus is projecting, with a slight midorbital reduction, and the squama indicates a relatively flat frontal. The frontal sinus seems restricted to the torus, and all these features indicate the specimen was a Neandertal. There is no direct dating on the specimen, and the oft-cited 50–60 ka date derives from the specimen’s similarity to specimens like La Chapelle-aux-Saints.

Regardless of the specimen’s date, this specimen shows that Neandertals extended farther north in Central-Western Europe than was previously demonstrated by paleontological evidence. If the 50–60 ka time range proves reliable, it would mean that Neandertals were able to adapt to harsher conditions than previously demonstrated. Although the Zeeland Ridges dating is uncertain, the fact they were inhabiting territory usually submerged in more temperate periods suggests they may have been here during colder times. Tools, potentially made by Neandertals, are found off the coast of East Anglia in Britain (Keys, 2008), suggesting Neandertals ranged even farther north; but these finds are undated and do not help indicate exactly when Neandertals were there. Isotopic analysis of the Zeeland Ridges specimen indicates a diet similar to that indicated for Neandertals in Germany and Belgium (Hublin et al., 2009).

Sarstedt

In 1986, three hominin cranial fragments along with artifacts were discovered during suction dredging of gravel deposits in the Leine River valley south of Hannover, Germany, at the site of Sarstedt (Czarnetzki et al., 2001, 2002). Although their exact age is far from clear, they most likely derive from a warm period during the Weichsel or Eemian glaciations. Although not clearly associated with the human remains, the artifacts indicate either Lower or Middle Paleolithic.

The three fossils comprise a juvenile temporal (Sst I), an occipital fragment (Sst II) with clearly Neandertal anatomy, and a piece of left parietal (Sst III) (Czarnetzki et al., 2001). Czarnetzki and colleagues (2001) contend that the temporal, despite an estimated 2–4 years of age at time of death, is likely female based on petrous anatomy. The small mastoid and proportions of the surrounding anatomy clearly align it with Neandertal juveniles such as Krapina 1. Furthermore, Czarnetzki and colleagues note two pathological conditions, hydrocephalus internus as well as non-specific meningitis. The Sarstedt II occipital piece exhibits lambdoidal flattening and commensurate occipital bunning, a suprainiac fossa, and an occipital torus, all of which align it with Neandertals. Finally, the Sarstedt III parietal fragment also aligns with Neandertals in its meningeal arterial pattern as well as its curvature (Czarnetzki et al., 2001). Thus, the Sarstedt remains are clearly Neandertal although, without better chronological context, little more can be said.

Hohlenstein-Stadel

Other fragments of Neandertals have been found in western Central Europe during the years since 1984 (Street et al., 2006). A right femoral diaphysis was recovered from

Hohlenstein-Stadel (Swabian Jura) in 1937 but was first analyzed by Kunter and Wahl in 1992. This specimen lacks both epiphyseal ends, but the shaft is well preserved. It lacks a pilaster, giving the specimen a characteristically Neandertal cross-section. The specimen also exhibits a distinct proximal-lateral femoral flange, a characteristic feature for European Neandertals (Cartmill and Smith, 2009). The Hohlenstein-Stadel femur was found in a dark layer in association with fauna correlated to the Eemian (OIS 5), suggesting an age of ~70–120 ka (Kunter and Wahl, 1992).

Hunas

In southeastern Bavaria, the site of Hunas has produced an isolated lower right molar, possibly an M_3 from layer F2 and in direct association with Pleistocene fauna and Middle Paleolithic artifacts (Alt et al., 2006).⁷ A speleotherm at the base of the deposits is dated to 76–79 ka by TIMS-U/Th (Alt et al., 2006; Rosendahl et al., 2011). The tooth is younger than this date range, but it is not possible to specify how much younger. First described 20 years earlier (Groiß, 1986), the molar is moderately worn and essentially complete. Alt and colleagues note correctly that the absence of taurodontism in Hunas does not preclude a Neandertal classification (Smith et al., 2006) and consider that the dimensions, enamel thickness, presence of a C-6 cusp, and other features are commensurate with assignment of the specimen to a Neandertal. Kupczik and Hublin's (2010) analysis of the molar root morphologies of Neandertals and modern humans places the Hunas tooth with the latter, yet this may just further demonstrate overlap of the two populations.

Sesselfelsgrötte, Klausennische, and Untere Klause

Also in Bavaria, three caves in the Altmühl Valley (Sesselfelsgrötte, Klausennische, and Untere Klause) have yielded fragmentary Neandertal remains (Rathgeber, 2003; Street et al., 2006). In Sesselfels, two deciduous teeth (both lost at about 12 years of age) and a partial postcranial skeleton of a probable fetal skeleton come from three different levels (Orschiedt, 2000). Unfortunately these have not been described in detail. The skeleton and one tooth derive from the G complex at the site and are associated with TL dates of 51–61 ka and radiocarbon dates that span a larger range but cluster at 46–48 ka (Richter, 2002). The second tooth comes from the earlier level M, with TL dates from 61 to 91 ka (Richter, 2002). Street and colleagues (2006) describe the Untere Klause specimen as the acromial end of a Neandertal clavicle and the Klausennische specimen as a deciduous lower central incisor associated with tools typical of the Middle Paleolithic in much of Germany.

Warendorf-Neuwarendorf

Further northwest, at Warendorf-Neuwarendorf, near Münster and just east of the Rhine, an anterior right parietal was discovered in so-called bone gravels (Czarnetzki and Trellisó-Carreño, 1999). The specimen is purportedly associated with Pleistocene fauna and Middle Paleolithic artifacts, but there is some uncertainty as to the parietal's stratum of origin (Street et al., 2006). The specimen is assigned to an interstadial in OIS 4 at ~50–70 ka, although this must be viewed as an estimation. The Warendorf parietal is described as being practically identical to the specimens from La Chapelle-aux-Saints and Feldhofer in terms of relative curvature and has an archaic pattern of the middle meningeal artery impressions on the bone's internal table, leading Czarnetzki and Trellisó-Carreño (1999) to designate the specimen as a Neandertal. In addition, Scholtz and colleagues (2000) identified a Neandertal genetic signal from this specimen using the southern blot hybridization technique.

Ochtendung

Positioned slightly west of the Rhine but still lying in the greater Rhineland Basin is a partial Neandertal cranium from Ochtendung (von Berg, 1997a, 1997b; von Berg et al., 2000). Ochtendung was recovered close to deposits of Middle Paleolithic tools and Pleistocene fauna (von Berg, 1997b). Von Berg and colleagues (2000) also reported the specimen was found in association with three purportedly Middle Paleolithic tools, and it is considered likely that the Ochtendung skull derives from deposits of the Saal glacial period—OIS 6. The specimen is a frontal and anterior parietals of an adult (probably male) individual, but the supraorbital region is unfortunately missing. The sagittal curvature is described as slight, with a low position and weak development of the parietal tuber (indicating a characteristically Neandertal oval coronal profile). Furthermore, the marked thickness of the specimen, and its large overall size (Condemi, 1997; von Berg et al., 2000) are commensurate with a Neandertal designation.

Neandertal Fossils from Eastern Central Europe

Unlike the case for western Central Europe, hardly any new sites have yielded Neandertal fossils in eastern Central Europe since Smith's 1984 review. A partial mandible from Mala Balanica (Serbia), originally thought to be Neandertal-aged (Roksandic et al., 2011), is now much too early (Rink et al., 2013), while the age and affinities of a single canine from Crvena Stijena (Montenegro) are uncertain (Roksandic, personal communication; R. Whallon, personal communication).⁸ Although new, important specimens have been described from the previously known sites of Krapina and Vindija and a new locality at the site of Šal'a, the major contributions have come in the form of new analyses of previously known fossils.

Neandertal Fossils from Moravia

Smith's (1984) descriptions of the Ochoz and Šipka fossils from Moravia remain valid today, and little further analysis has been conducted on these fragmentary remains. The Ochoz fossils⁹ comprise a mandible, two cranial fragments, and a molar (Smith, 1984; Vlček, 1969), while the Šipka fossil is a mandibular symphysis piece. Anatomically, both fall with Neandertals.

Šal'a

The frontal bone from the Slovakian site of Šal'a was discovered in 1961 (Smith, 1984; Vlček, 1969). In the mid-1990s, a left parietal and portion of a frontal bone (Šal'a 2) were found in secondary deposits along the Váh River near the find spot of the 1961 specimen (Jakab, 1996; Sládek et al., 2002). Jakab (1996) identifies these new remains as Neandertal. Reinvestigation of the Šal'a site's biostratigraphy indicates that the fossils date to OIS 5e, making them similar in age to the Neandertals from Krapina and Ganovce (Sládek et al., 2002).

Early interpretations of Šal'a 1 (Jelínek, 1969; Smith, 1982, 1984; Vlček, 1969) saw it as representing a transitional population between more robust Neandertals and Upper Paleolithic modern humans. Key to this interpretation was the overall thinness of Šal'a's supraorbital torus with its midorbit pinching (Smith and Ranyard, 1980). Furthermore, Wolpoff (1999) contended that the Šal'a 1 frontal was just as similar to the Skhül-Qafzeh

hominins as it was to Neandertals. However, a recent morphometric analysis (Sládek et al., 2002) demonstrates that the Šal'a specimen is most like Neandertals. In some respects, it is similar to the Skhül-Qafzeh fossils, but its sagittal curvature and supraorbital morphology are more like Neandertals.

Suba-lyuk

Adult and juvenile fossils associated with La Quina type Mousterian artifacts were discovered in 1932 at the cave site of Suba-lyuk (Hungary) (Bartucz et al., 1940; Mester, 2004; Tillier et al., 2006). Based upon faunal evidence, the remains may date to OIS 4 (Ringer, 1993), although, as Tillier and colleagues (2006) point out, this needs to be confirmed by absolute dating. The adult fossils (Suba-lyuk 1) comprise a partial mandible as well as teeth and some postcrania (Smith, 1984). It is unclear whether or not these adult remains belong to the same individual (Tillier et al., 2006). Suba-lyuk 2 is the partial cranium and isolated teeth of an approximately 3-year-old child (Tillier et al., 2006). Anatomically, the Suba-lyuk specimens align with Neandertals, although Pap, Tillier, and colleagues (Pap et al., 1996; Tillier et al., 2006) emphasize their mosaic appearance and stress that the Suba-lyuk fossils demonstrate the variability of Middle Paleolithic Europeans.

Krapina

The largest sample of Neandertal skeletal remains from Central Europe comes from deposits removed from a rock shelter on Hušnjakovo Brdo (Hušnjak Hill) on the outskirts of the town of Krapina in northern Croatia. The site was excavated between 1899 and 1905 by the eminent Croatian paleontologist Dragutin Gorjanović-Kramberger. Gorjanović published just under one hundred papers on Krapina from 1899 until 1929, but his best-known work is a detailed monograph published in 1906. Gorjanović's work at Krapina has been assessed by Radovčić (1988), who situates this work in a historical and current context.

The impressive Krapina sample continues to be a wealth of information about Neandertals (Frayer, 2006; Frayer et al., 2007). The papers, books, theses, and dissertations focusing on this collection since Smith's (1976b) pioneering work are far too many to list and cover fully here. Since Smith's 1984 overview of the site, the skeletal sample has grown from just under nine hundred to over a thousand elements, mainly through careful searching of the faunal sample from the site. These additional fossil identifications and associations (Ahern, 2006b; Caspari and Radovčić, 2006; Minugh-Purvis et al., 2000; Radovčić et al., 1988) have added to the already unparalleled perspective on populational variation within Neandertals. Unfortunately, most specimens are isolated teeth, complete smaller bones (especially hand and foot bones), and fragments of other bones. Krapina has five informative partial crania and some eleven maxillae and twelve mandibles (excluding sixteen rami) in various states of completion. There are, however, relatively large samples of specific bones or parts of bones that have allowed a fuller understanding of various aspects of Neandertal anatomical variability. A systematic catalog of the Krapina hominin remains was published in 1988 (Radovčić et al., 1988), and an updated edition is currently in press.

Several other informative publications by the Croatian Natural History Museum followed the 1988 skeletal catalog. A radiographic atlas of the collection was published 11 years later (Kricun et al., 1999). A systematic bibliography for the years 1899 through 2004 was assembled for the centennial of the publication of Gorjanović's 1906 monograph (Frayer, 2006). A series of thirty-two papers on various aspects of the Krapina sample were published by the Croatian journal *Periodicum Biologorum*, also in 2006; and 2 years later these were reprinted in a volume published by the Croatian Natural History Museum (Monge et al., 2008).

Finally, a thorough analysis of the fauna from Krapina and what these remains can tell us about certain aspects of Neandertal behavior is provided by Miracle (2007).¹⁰ These and other publications since 1984 reflect the openness of the Krapina collection for research by qualified scientists regardless of their theoretical orientation. This continued open access policy has resulted in a great deal of important research and has enhanced the importance of the Krapina collection for the understanding of Neandertal paleobiology.

One of the most significant changes in our knowledge about Krapina involves the age of the deposits. Gorjanović recognized thirteen stratigraphic levels at the site, with eight containing Mousterian artifacts and human skeletal elements (Gorjanović-Kramberger, 1906; Simek and Smith, 1997; Smith, 1976b). Based on his observation that the rock shelter matrix at Krapina disintegrated rapidly, Gorjanović (1913) estimated that the culture-bearing deposits accumulated over about an 8,000-year period. Based on the fauna, he (1906) assigned the deposits to a warm, interglacial period. More recent analysis by Malez (1978) concluded that the deposits represented a much longer period, stretching from the last interglacial until well into the last glaciation, perhaps into mid-OIS 3. Malez's perspective had important implications for the fossil human remains. While the majority of the remains derive from levels 3 and 4, Gorjanović's "Homo Zone" correlated to the last interglacial (OIS 5e); isolated finds were also found in levels 5–7, with a second mini-concentration of hominin fossils in level 8 (Radović et al., 1988; Smith, 1976b). Except for the level 8 remains, all of the other specimens were definitively Neandertal in morphology, and no evidence for change over time could be identified (Smith, 1976b). However, if level 8 was really "late," the suggestion of "transitional" anatomy in the remains from this level would take on added significance (Minugh-Purvis et al., 2000).

In 1995, Rink and colleagues presented a series of ESR dates for the Krapina site. The dates from levels 1, 5–6, and 7–8 are indistinguishable from each other and clustered about a mean of 130 ± 10 kya, which indicates the entire sequence was deposited within OIS 5e, the last interglacial. Miracle's faunal analysis indicates that habitation at Krapina extended beyond the last interglacial (OIS 5e) into the subsequent colder stage of 5d (Miracle, 2007). He notes no support for Malez's extended habitation through the later Würm but suggests that the extent of occupation may have been around 20,000 years, from 130 to 110 kya (Miracle, 2007). Analysis of the Krapina lithics reveals a behavioral shift from levels 3/4 and level 8 in material procurement and in site use but nothing that falls out of the realm of Neandertal behavior (Simek and Smith, 1997). In total, this new evidence supports Gorjanović's perspective on the age and length of occupation of the site.

The dating firmly establishes Krapina as an "early" Neandertal sample. It also specifically impacts the interpretation of the level 8 remains. Most prominent is the Krapina (Kr 1) cranium, also known as the A skull. It is a partial calvarium of a juvenile, aged 6–8 years (Minugh-Purvis et al., 2000; Smith, 1976b). The specimen has been suggested to show progressive features compared to other Neandertals (cf. Škerlj, 1958), particularly in frontal curvature, frontal boss development, glenoid fossa morphology, and browridge shape and development. Detailed analysis of these and other features, however, demonstrates that all can be matched in other Neandertals (Minugh-Purvis et al., 2000). Thus, the total morphological pattern, viewed in a comparative context, "strongly supports the contention that Krapina 1 derives from a European Neandertal population" (Minugh-Purvis et al., 2000: 422). Therefore, the evidence indicates that all of the Krapina hominin skeletal remains are Neandertals, commensurate in morphology with their relatively early age. Again, this result supports Gorjanović's interpretation that more modern humans were not present at Krapina (Gorjanović-Kramberger, 1913).

Debate still surrounds the predepositional treatment of the Krapina human bones. Some have argued that the bones show evidence of human processing, perhaps related to dietary



Figure 5.5. Krapina 3 frontal bone exhibiting a series of cutmarks that Frayer and colleagues (2008) have interpreted as a funereal behavior not related to cannibalism or defleshing. Each number labels one of the thirty-five identified cutmarks. Image from Frayer et al. (2008) and courtesy of D. W. Frayer.

cannibalism (White, 2001), while others have interpreted the level of preservation of the remains as requiring some form of burial (Russell, 1987a,b; Trinkaus, 1985). To some extent, both may be true. Most investigators have recognized some post-mortem manipulation of the Krapina human remains (see discussion in Smith, 1976b), including the recent suggestion of ritual treatment of the Krapina C (Kr 3) skull (Figure 5.5; Frayer et al., 2008). Gorjanović (1904) noted that the manner of breakage and burning of the human bones reflects an “Akt des Kannibalismus.” In his description of the Krapina deposits in the same publication, Gorjanović notes that animal bones were discarded toward the walls of the rock shelter rather than the center. He then states that the human bones were treated in the same manner and that these bones were preserved in concentrated bone middens (“Knochenhaufen”) near the walls of the rock shelter (Gorjanović-Kramberger, 1904). This circumstance contributed to the state of preservation of the fragmentary remains, both animal and human, at the site. Thus the “burial” of the Krapina human bones may not relate to any form of intentional interment.

The description of the Krapina people provided earlier (Smith, 1984) is fundamentally accurate today, although it has certainly been enhanced by many subsequent studies (Monge et al., 2008). That description noted that despite the variation present in the Krapina sample, no feature or specimen in that sample falls outside the Neandertal morphological realm, a conclusion also emphasized in recent discussions (Cartmill and Smith, 2009; Schwartz and Tattersall, 2008). Some studies have enhanced the Neandertal signature of the Krapina remains particularly in the clavicle (Voisin, 2008), posterior dentition (Bailey, 2008) and occipital bones (Caspari, 2008). In the latter context, reconstruction of the rear vault of Krapina 5 (Figure 5.6) demonstrates the presence of occipital bunning in adult specimens at the site, a condition already documented for the subadult Krapina 2. Pearson and Busby (2008) find that many postcranial aspects of the Krapina sample do not exhibit the extent of development of later “classic” Neandertals. However, there is a strong possibility of an overabundance of females in the sample (Ahern, 2008). Thus the perceived differences noted by Pearson and Busby (2008) are likely due to a sex bias in the sample. Overall then, there is nothing at Krapina that questions their recognition as “typical” Neandertals in terms of morphology or behavior.

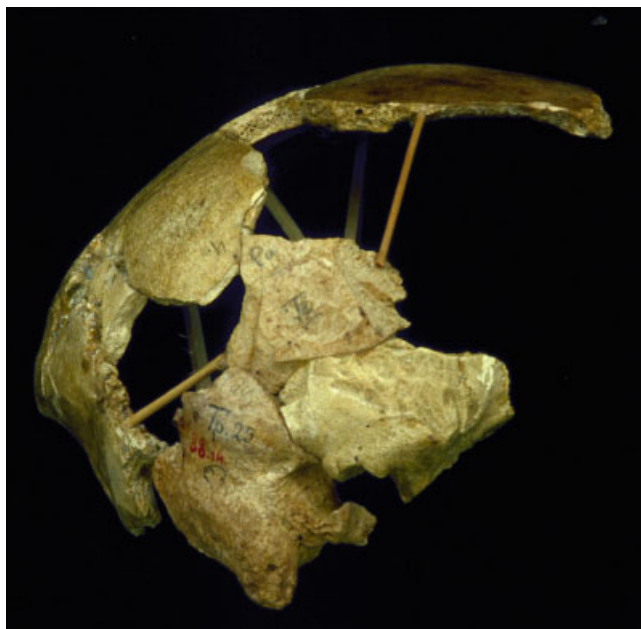


Figure 5.6. The Krapina 5 reconstruction by Caspari and Radovčić (2006) showing the three newly associated temporal pieces. Image courtesy of R. Caspari.

Vindija

Excavations at Vindija Cave (Croatia) during the 1970s and 1980s yielded late Mousterian and early Upper Paleolithic human remains representing the best evidence about late Neandertals in Central Europe (Janković et al., 2006; Malez and Ullrich, 1982; Wolpoff et al., 1981). While the majority of the Vindija collection was described in 1981 (Wolpoff et al., 1981), additional specimens were published in later years (Ahern et al., 2004; Smith and Ahern, 1994; Smith et al., 1985). Although fragmentary, multiple individuals are preserved for many anatomical elements, especially in the case of mandibles and frontal bones. This has made Vindija the focus of numerous analyses from the 1980s onward.

All of the Pleistocene Vindija hominin fossils with known provenience derive from stratigraphic complexes G and F.¹¹ Most of these specimens come from level G₃ within the G complex, while the remainder derive from G₁, F_d or F_{d/d}. Archaeologically, the G and F deposits span the Middle to Upper Paleolithic transition, with level G₃ containing a late Mousterian assemblage, G₁ an initial Upper Paleolithic assemblage,¹² and F_d and F_{d/d} an Aurignacian-like assemblage. Over time within the Mousterian sequence of the site there is an increase in the frequency of the Upper Paleolithic elements and higher quality raw materials (Ahern et al., 2004; Janković et al., 2006, 2011). Parallels for this can be seen within the Late Mousterian of neighboring Italy (Peresani, 2011).

Chronologically, level G₃ likely represents the Lower Würm stadial (~38–45.6 ka) based upon the composition of the fauna as well as direct AMS radiocarbon dating of two hominin specimens (> 42 ka ¹⁴C BP, Krings et al., 2000; 38.31 ± 2.31 ka ¹⁴C BP, Serre et al., 2004) as well as a U-Th (41.0 ± 1.0/–0.9 ka BP, Wild et al., 2001) dating of cave bear bone. The chronology for level G₁ appears to be somewhat more complex. Sedimentologically, G₁ is a reddish-brown clay that is distinct in the Vindija sequence. This clay represents a warmer



Figure 5.7. A split-based bone point (Vi 3437) and a diagnostically Neandertal mandibular ramus (Vi 207) excavated from level G_1 at Vindija Cave. Direct ultrafiltration AMS ^{14}C dating of the ramus provided a date that is consistent with the early Upper Paleolithic. Attempts at direct dating the point have, thus far, not been successful. The scale is 1 centimeter.

period and has been suggested to be from the Podhradern interstadial (Musil and Valoch, 1966) in age (Ahern et al., 2004; Wolpoff et al., 1981). The radiometric dates for G_1 , including direct AMS and ultrafiltration AMS dates on two of the Neandertal specimens as well as AMS radiocarbon and U-Th dates on cave bear bones, indicate that the deposits date to sometime between 29 and 34 ka. Two radiocarbon dates, both from cave bear bone, have yielded spuriously young (18.28 ± 0.44 ka ^{14}C BP, Z-2432, Obelić et al., 1994) and old ($46.8 \pm 2.3/-1.8$ ka ^{14}C BP, VERA-1428, Wild et al., 2001) dates. Although the younger non-AMS date is likely due to contamination by young carbon, the older date highlights the possibility that the G_1 collection includes items mixed in from under- and/or overlying levels via cryo- and/or bioturbation (Zilhão, 2009). Such possible mixture has been used to explain away the apparent Neandertal–Upper Paleolithic association in level G_1 (Kozłowski, 1996; Montet-White, 1996; Stringer, 1982; Zilhão, 2009; Zilhão and d’Errico, 1999). None of the artifacts recovered from G_1 exhibit characteristics consistent with such movement (Karavanić and Smith, 1998) and the Upper Paleolithic split-base bone point (Figure 5.7) and most of the Neandertal fossils came from areas in the cave lacking any observable cryoturbation (Wolpoff et al., 1981). Furthermore, the direct AMS radiocarbon dates of two of the G_1 hominin fossils are consistent with an early Upper Paleolithic age (Higham et al., 2006). However, recent lithic refitting analysis by Bruner (2009, 2011) clearly indicates more level mixing than had previously been realized. Furthermore, attempts to directly date the typologically Aurignacian split-base bone point (Figure 5.7) from G_1 have thus far proven futile. Nevertheless, it is important to keep in mind that, for those hominin remains that have been directly dated, these dates have been consistent with the fossils’ level designations (i.e., G_3 fossils date older than G_1 ones; but see Zilhão, 2009). Finally, a cave bear bone from level $F_{d/d}$ has been radiocarbon dated to 26.6 ± 0.93 ka ^{14}C BP (Z-2433, Obelić et al., 1994), while three other dates on charcoal from complex F range from 24 ± 3.3 ka ^{14}C BP to 29.7 ± 0.6 ka ^{14}C BP. Although these dates are fairly consistent, the presence of Neandertal-like hominin remains from $F_{d/d}$ and F_d combined with Bruner’s (2009, 2011) work suggests that some mixing may have affected the F complex. Unfortunately, we may never have a precise

understanding of the chronology of all of the fossils, artifacts, and fauna from Vindija. Further direct dating of the hominin remains and, perhaps, bone artifacts may improve our understanding, but questions will likely always remain.

Early interpretations of the biology of the Vindija late Neandertals, such as those by Smith (1982, 1984), posited that the Vindija sample represented a population transitional between earlier Neandertals, such as those represented at Krapina, and Upper Paleolithic modern humans. Aspects of the Vindija remains that appear intermediate include reduced midfacial prognathism, reduced nasal breadth, thinner cranial vaults, reduced postorbital constriction, development of incipient chins, reduction and shape changes in the supraorbital region, a broad braincase relative to upper facial breadth, a higher vault with a more vertical forehead, and a modern-like scapular glenoid breadth (Ahern, 1998; Ahern et al., 2002, 2004; Smith, 1982, 1984; Smith and Ranyard, 1980; Smith and Trinkaus, 1991; Wolpoff et al., 1981).

Although Vindija's morphological intermediacy was interpreted by many as evidence of an evolutionary transition from Neandertals to modern humans, others offered alternative explanations. Howell (1984) and others (Bräuer, 1989, 1992; Klein, 1999; Stringer et al., 1984) suggested that the morphological intermediacy of the Vindija hominins stemmed from an overabundance of females and/or juveniles in the sample or that the Vindija population had small body size compared to other Neandertals and thus were more gracile than the earlier Neandertals from Krapina. However, simulation analyses as well as comparisons with extant referent populations demonstrate that neither sex- nor age-related sample bias is a likely explanation of the Vindija sample's intermediacy (Ahern, 2006b; Ahern et al., 2002; Ahern, 1998; Ahern and Smith, 2004; Kesterke and Ahern, 2007). Furthermore, the body sizes of the Vindija hominins were not significantly smaller than other Neandertals (Trinkaus and Smith, 1995). Although the morphological intermediacy of the Vindija late Neandertals may have not been evolutionary but caused by independent factors (Klein, 2009), we contend that gene flow with modern populations is the most parsimonious explanation.

As chronological revisions and new genetic and fossil data during the late 1980s and 1990s called into question equipolycentric explanations of modern human origins such as classic Multiregional Evolution, newly identified fossils from Vindija combined with new analyses, including the direct AMS ^{14}C dating of some of the remains discussed above, have required a rejection of the idea that the Vindija population was an intermediate step in a gradual evolution of Neandertals into modern humans. What has resulted is a more nuanced interpretation of the Vindija sample (Ahern et al., 2004; Janković et al., 2006, 2011). Some of the Vindija fossils published since the 1980s, such as the gracile Vi 308 medial supraorbital (Smith and Ahern, 1994) and the Vi 284-255-256 partial calotte (Figure 5.8; Ahern et al., 2004) confirm the sample's morphological intermediacy, while other specimens, such as the robust Vi 307 zygomatic (Smith and Ahern, 1994) and the Vi 13.8 radius (Ahern et al., 2004) fall well within the Neandertal range of variation. While the more modern-like aspects of the late Mousterian-associated Neandertals from Vindija likely reflect gene flow from outside of the region prior to any significant modern colonization of Europe, the persistence of level G_1 specimens with Neandertal gestalt at approximately 29–34 ka (Higham et al., 2006) possibly associated with an initial Upper Paleolithic industry indicates a complex biocultural scenario (Ahern et al., 2004; Janković et al., 2011). Ahern and colleagues (2004) suggest that the Vindija evidence is consistent with a scenario whereby Neandertals, as illustrated by the Krapina – Vindija sequence, changed over time through gene flow and common selection with contemporary peoples, but that some European populations, including those represented by the G_1 (and possibly F) hominins, remained identifiably Neandertal upon the arrival of intrusive modern humans.

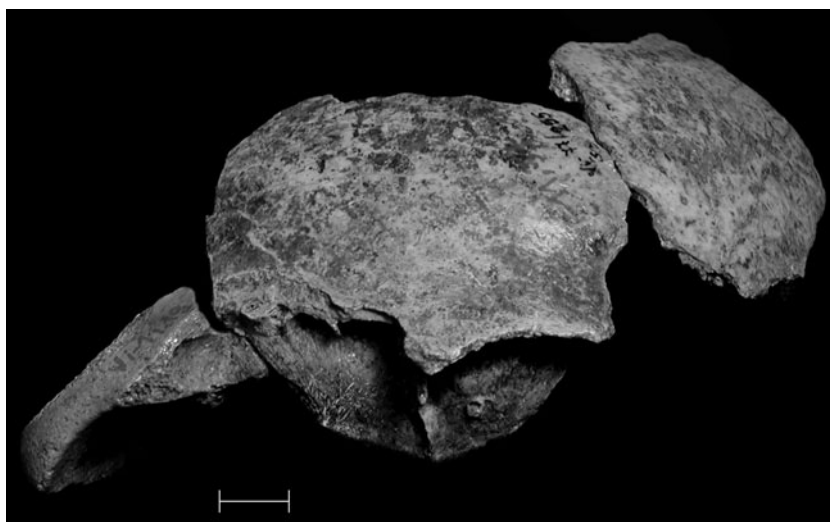


Figure 5.8. Vindija 284-255-256. This is the most complete cranial specimen from Vindija Cave. A fourth piece, the Vi 230 parietal, that was associated with Vi 256 by Wolpoff et al. (1981) and Ahern et al. (2004) is likely from a younger individual. The scale is 1 centimeter.

Mala Balanica

A recently discovered partial mandible from Mala Balanica, Serbia (Roksandic et al., 2011), raised questions about the pattern of Middle to Late Pleistocene evolution in southeastern Central Europe. The mandible, comprising a piece of left corpus preserved from the canine alveolus to the anterior margin of the ramus, exhibits a suite of characteristics that align it more with Early and Middle Pleistocene *Homo* than with Neandertals (Roksandic et al., 2011). Most surprisingly, the original interpretation of the archaeological, geological, and radiometric evidence suggested possible contemporaneity with the OIS 5e Krapina Neandertals (Roksandic et al., 2011). However, recent ESR dating of associated animal teeth provided an estimated age of at least 397–582 ka BP (Rink et al., 2013). Thus, Mala Balanica's primitive anatomy must be considered within the context of Middle Pleistocene human evolution and is not directly relevant to modern human origins in Central Europe.

Stajnia

Stajnia Cave (Poland) is located in the highlands about 100 km north of the Carpathian Mountains. At this site, three human teeth were excavated from deposits yielding Middle Paleolithic (Micoquian) artifacts and Pleistocene fauna. A cave bear bone from these deposits yielded an AMS radiocarbon age of >49 ka; and the overall archaeological and faunal context suggests an age of either late OIS 6 or 5d (Urbanowski et al., 2010), which could mean an age in excess of 100 ka. One tooth, a right M², has been described to date, with the others still in analysis. The molar is heavily worn, thus precluding the identification of specifically Neandertal crown morphology, but crown dimensions, hypocone size, and pattern of relative cusp sizes are commensurate with Neandertal affiliations (Urbanowski et al., 2010). Urbanowski and colleagues also report that DNA was extracted from the specimen. This yielded a male genotype not typical of recent humans or chimpanzees, but the sample was too degraded to allow conclusive determination of Neandertal affinities.

Neandertals of the Initial Upper Paleolithic?

Artifact assemblages, exhibiting a mixture of Middle and Upper Paleolithic elements and dating to the Hengelo interstadial and the beginning of the following stadial, have been described from a variety of sites across Eastern and Central Europe. These assemblages are characterized by the presence of leaf-shaped points and can be classified as Szeletian *sensu lato* (cf. Allsworth-Jones, 1986; Churchill and Smith, 2000). Only three sites have any hominin remains found in association with these “transitional” assemblages: Vindija, Dzeravá Skála, and Remete-Felső (Figure 5.3 and Table 5.3). Vindija has only one Szeletian tool.

At Vindija, diagnostically Neandertal remains; Mousterian, Szeletian, and Aurignacian lithics; and bone points (including a split-base one, Figure 5.7) were recovered from level G₁ (Ahern et al., 2004; Smith and Ahern, 1994; Wolpoff et al., 1981). These co-occurrences may have been the result of mechanical mixing of sediments (Allsworth-Jones, 1986; Bruner, 2009, 2011; Zilhão, 2009; Zilhão and d’Errico, 1999). However, as discussed above, there are compelling reasons to accept a co-occurrence of Neandertal remains and initial Upper Paleolithic artifacts at Vindija. One reason, not discussed above, is that the Vindija situation is not unique (Svoboda, 2005). Aurignacian-like bone and antler points have been found in association with Szeletian points at Mamutowa, Istálloskö, Szeleta, and Dzeravá Skála in addition to Vindija level G₁ (Svoboda, 2005). As Svoboda (2005) notes, such archaeological associations are not easy to explain away as the result of mechanical mixing when they are found at so many sites.

The unerupted hominin mandibular molar from Dzeravá Skála, Slovakia, was discovered during the sorting of faunal remains after excavation (Allsworth-Jones, 1986; Hillebrand, 1914). Although likely an M₂, Bailey and colleagues (2009) suggest that an M₁ designation cannot be ruled out. According to Hillebrand (1914), the tooth exhibits a well-developed anterior fovea, like Neandertals. While Tillier and colleagues (2005) see the taxonomic attribution of this tooth as ambiguous, Bailey and colleagues’ (2009) analysis on non-metric aspects places the Dzeravá Skála tooth with Upper Paleolithic modern humans. As is the case with Vindija level G₁, the associated artifact assemblage is a mixture of Szeletian lithics and Aurignacian-like bone points (Hillebrand, 1914; Prošek, 1953). Also, like Vindija G₁, cryoturbation may have caused some level mixing at Dzeravá Skála (Prošek, 1953). Excavations at

Table 5.3. Central European human remains¹ associated with transitional assemblages (Szeletian *sensu lato*)

Site	Human Remains	Cultural Association	Date(s)	Date Reference(s)
Dzeravá Skála (Slovakia)	M ₁ or M ₂ germ ¹	Szeletian <i>sensu lato</i> ²	> 44.6 ky BP	Davies et al., 2005
Remete Felső (Hungary)	Two incisors and a canine ¹	Szeletian <i>sensu lato</i> ²	OIS 3	Gábori-Csák, 1983; Vörös, 2000; Tillier, 2006
Vindija—level G ₁ (Croatia)	Fragmentary cranial, dental, and postcranial remains	Szeletian <i>sensu lato</i> ²	OIS 3 30.6–34.2 ka* ³	Higham et al., 2006

*Direct date(s) on human remains.

¹ The taxonomic affinities of these remains is contentious. See text.

² Questions remain about the co-association of all of the artifacts and the human remains. See text.

³ Time span based on direct ultrafiltration AMS dates only (Higham et al., 2006). Earlier direct AMS (non-ultrafiltration) provided a time span of ≈28.7–29.6 ky BP (Smith et al., 1999).

Dzeravá Skála during 2002–2003 (Kaminska et al., 2005) focused on establishing a better chronology for the cave sediments, especially in regard to the Middle–Upper Paleolithic transition. Unfortunately only a single date was obtained for layer 11 (the Szeletian *sensu lato* level from which the tooth reportedly derives). This AMS radiocarbon date of >44.6 ka ^{14}C BP (OxA-13973, Davies and Hedges, 2005) is considerably older than the dates for other “transitional” industries in Central Europe. Davies and Hedges (2005) suggest that the layer 11 artifacts may actually be Middle Paleolithic rather than Szeletian, based upon this single date. The single, minimal date, combined with the taxonomic ambiguity of the hominin tooth and the potential that cryoturbation caused level mixing at the site, all undermine the importance of the Dzeravá Skála tooth for understanding modern human origins in Central Europe.

As was the case with the Dzeravá Skála tooth, the two right lower incisors and a canine from Remete Felső, Hungary, are reported to have been found among faunal remains that were found in association with twelve lithics (Gábori-Csánk, 1983; Tillier et al., 2006). The lithic assemblage appears to be a Szeletian variant (Gábori-Csánk, 1983). According to Tillier and colleagues (2006), the heavily worn Remete Felső teeth are morphologically undiagnostic in terms of whether they are Neandertal or modern human.

In sum, the Szeletian *sensu lato*–associated hominin remains are scarce. The Dzeravá Skála tooth may be modern-like but is not clearly so. Furthermore, its current dating seems to indicate that it may be Middle Paleolithic and not Szeletian at all. Although the Vindija G₁ fossils are the most numerous and the most diagnostic of the hominin remains associated with a “transitional” industry, questions remain about their co-occurrence with the Szeletian (*sensu lato*) artifacts. Finally, the population affinity of the Remete Felső teeth is ambiguous. Thus, it is possible that only Neandertals are associated with the Szeletian in Central Europe, but it seems to be equally possible that only modern humans are. If such an association is confirmed, it would appear to be similar to the situation on the Italian peninsula, where recent analysis of hominin deciduous molars associated with another “transitional” industry, the Uluzzian, indicates that they were from anatomically modern humans (Benazzi et al., 2011). Yet, as Riel-Salavatore and colleagues (2012) point out, it may be more productive to interpret the biology and culture associated with “transitional” industries in less typological terms than the Neandertal-modern and Middle–Upper Paleolithic dichotomies. Thus, it is possible that the ambiguous anatomy of the Szeletian *sensu lato* remains reflects varying degrees of traits that characterize earlier archaic and later modern populations.

The Central European Fossil Record of the Earliest Modern Humans

Since Smith (1984) reviewed the Central European early modern human fossil record, it has changed much more dramatically than has the Neandertal record. This has been in large part due to the application of AMS ^{14}C direct dating and redating of many fossils. Many fossils once thought to be Aurignacian or Gravettian have been demonstrated to be much more recent. In addition to chronological and sample changes, significant research has gone into better understanding previously known fossils, such as those from Dolní Věstonice, Pavlov (Sládek et al., 2000; Trinkaus and Svoboda, 2006), and Mladeč (Teschler-Nicola, 2006). Finally, and perhaps most importantly, the fossils discovered from Peștera cu Oase are currently the oldest known modern human fossils from Europe and exhibit a mosaic of modern and archaic anatomy (Rougier et al., 2007; Trinkaus et al., 2003b). The Oase discoveries have thrown fresh light upon the Romanian early modern human record, resulting in the recent direct dating of and reanalysis of the remains from Cioclovina (Harvati et al., 2007) and Muierii (Soficaru et al., 2006). Table 5.4 lists early modern human fossils from Central Europe, while Figure 5.9 maps their locations.

Table 5.4. Early modern human remains from Central Europe.

Site	Human Remains	Cultural Association	Date(s)	Date Reference(s)
Western Central Europe				
<i>Pre-Gravettian</i> (all from Germany)				
Hohlenstein-Stadel	Premolar	Aurignacian?		Orschiedt, 2000; Street et al., 2006
Geißenklösterle	Deciduous tooth	Aurignacian?		Orschiedt, 2000; Street et al., 2006
Honerhöhle	Fragmentary cranial, mandibular, and dental [†]	Aurignacian?		Gielser, 1971; Street et al., 2006
Kleine Ofnet	Tooth	Aurignacian?		Orschiedt, 2000; Street et al., 2006
Schafstall	Molar	Aurignacian?		Orschiedt, 2000; Street et al., 2006
Schelklingen, Ulm	Left mandibular molar & canine	Aurignacian?		Street et al., 2006
Sirgenstein	Right C ¹	Aurignacian?		Street et al., 2006
<i>Gravettian</i>				
Geißenklösterle	Two deciduous teeth	Gravettian		Pasda & Hahn, 1991; Street et al., 2006
Hohle Fels	Deciduous molar & cranial fragment	Gravettian		Haas, 1991; Street et al., 2006
Eastern Central Europe				
<i>Pre-Gravettian</i>				
Bacho Kiro (Bulgaria)	Cranial and mandibular fragments, isolated teeth	Lv 11: "Proto-Aurignacian" Lv 6–7: Aurignacian	Lv 11: $\approx 32.9\text{--}40.2\text{ ka}$ Lv 6–7: $\approx 28.2\text{--}33.0\text{ ka}$	Hedges et al., 1994
Bordu Mare (Romania)	Three phalanges ³	Aurignacian? ¹		Alexandrescu et al., 2010
Cioclovina (Romania)	Calvarium	Unclear	$28.5 \pm 0.2\text{ ky BP}^*$	Soficaru et al., 2007
Görömböly-Tapolca (Hungary)	Occipital	?	$30.3 \pm 0.3\text{ ky BP}^*$	Tillier, 2006; Davies & Hedges, 2008–2009
Istállóskő (Hungary)	M ₁ or M ₂ germ ³	Aurignacian ¹	$\approx 39.7\text{ ka}^1$	Allsworth-Jones, 1990; Tillier, 2006
La Adam (Romania)	Molar germ	Aurignacian? ¹		Alexandrescu et al., 2010
Mießlingtal (Austria)	Juvenile mandibular symphysis	Aurignacian (Late?) ¹		Felgenhauer, 1950; Churchill & Smith, 2000
Mladeč (Czech Rep.)	Cranial and postcranial remains from multiple individuals [†]	Aurignacian (Middle to Late)	$30.7\text{--}31.5\text{ ky BP}^*$	Wild et al., 2005, 2006

Malu Roșu (Romania)	Frontal fragment	Aurignacian? ¹		Alexandrescu et al., 2010
Oblazowa (Poland)	Distal thumb phalanx	?	31.0 ± 0.55 ky BP*	Hedges et al., 1996
Peștera Mică (Romania)	Femoral fragment	Aurignacian? ¹		Alexandrescu et al., 2010
Peștera cu Oase (Romania)	Mandible (Oase 1) and cranium (Oase 2)	None	1: 34.3 ± 1.0/-0.9 ky BP* 2: 28.9 ± ∞/-170 ky BP*	Trinkaus et al., 2003; Rougier et al., 2007
Peștera Muierii (Romania)	Skull, temporal and postcranial remains	Mousterian? ²	M1: 30.2 ± 0.8 ky BP* M1: 29.9 ± 0.2 ky BP* M2: 29.1 ± 0.2 ky BP*	Soficaru et al., 2006; Dobos et al., 2010
Vindija – F complex (Croatia)	Three anterior teeth, two articulating parietals ³	Aurignacian?	≈20.7–31.7 ka ¹	Srdoc et al., 1984
<i>Gravettian</i>				
Brno-Franzouská (Czech Rep.)	Calvarium and postcrania	Gravettian (Willendorf-Kostienkian)	22.8 ± 0.2 ky BP*	Pettitt & Trinkaus, 1999
Dolní Věstonice (Czech Rep.)	Five associated skeletons plus numerous other cranial, dental, and postcrania remains ¹	Gravettian (Pavlovian)	≈23.1–27.2 ka ⁴	Svoboda, 2006
Grub/Kranawetberg (Austria)	Two deciduous tooth fragments	Gravettian (Willendorf-Kostienkian)	24.4–25.5 ka	Antl-Weiser, 1999; Antl-Weiser & Teschler-Nikola, 2000/2001
Krems-Wachtberg (Austria)	Three infant skeletons	Gravettian (Willendorf-Kostienkian)	26.6 ± 0.2 ky BP	Einwögerer et al., 2005, 2006
Pavlov (Czech Rep.)	Associated skeleton (Pavlov 1), maxilla, mandible, mandibular fragment, and twenty-six isolated teeth	Gravettian (Pavlovian)	26.2 ± 0.5 ky BP	Svoboda, 2006
Předmostí (Czech Rep.)	Remains of approximately thirty individuals, at least two associated skeletons ¹	Gravettian (Pavlovian)	≈25–27 ka	Svoboda, 2001
Willendorf I & II (Austria)	I: Femoral diaphysis, II: mandibular symphysis	Mousterian	I: 24.3 ± 0.2 ky BP*	Teschler-Nikola & Trinkaus, 2001

¹ Some or all of the fossils are known to be missing or destroyed.

* Direct date(s) on human remains.

¹ Date is tentative and should be regarded with caution.

² The association of the Muierii skull with Mousterian artifacts is regarded as being due to level mixture (Dobos et al, 2010).

³ The taxonomic affinities of these remains is contentious. See text.

⁴ Range (including single errors) of radiocarbon dates from the Dolní Věstonice II site (Svoboda, 2006). Generally, the Dolní Věstonice remains are regarded as being ≈25–27 ka.

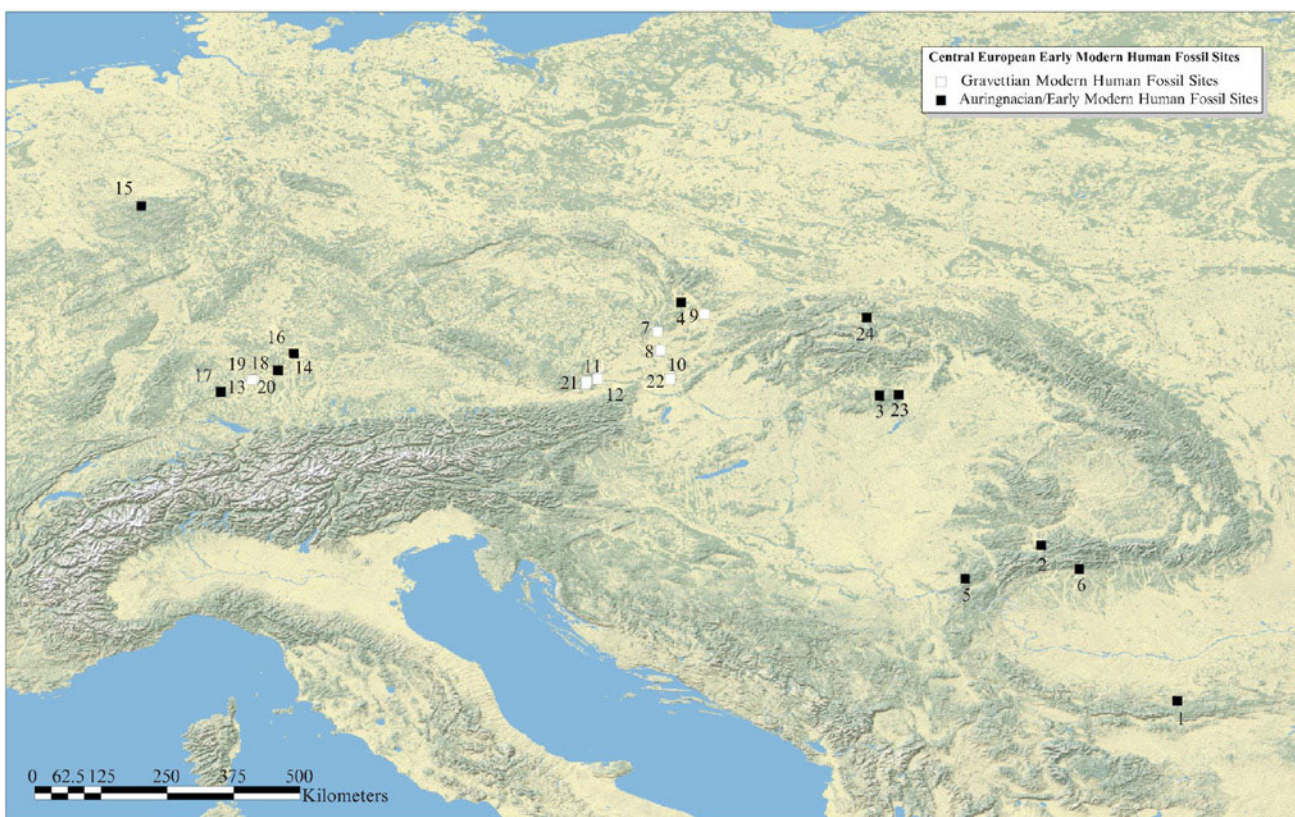


Figure 5.9. Aurignacian/early modern human fossil sites: * 1: Bacho Kiro; 2: Cioclovina; 3: Istállós-kő; 4: Mladeč; 5: Peștera cu Oase; 6: Peștera Muierii; 14: Hohlenstein-Stadel; 15: Honerthöle; 16: Kleine Ofnet; 17: Schafstall; 18: Sirgenstein; 19: Geißenkösterle; 21: Miesslingtal; 23: Görömby-Tapolca; 24: Oblazowa. Gravettian modern human fossil sites: 7: Brno-Fracoužská; 8: Dolní Věstonice; 9: Předmostí; 10: Pavlov; 11: Willendorf; 12: Krems-Wachtberg; 13: Geißenkösterle; 20: Hohle Fels; 22: Grub/Kranawetberg. *Four Romanian sites (*La Adam, Bordu Mare, Malu Roșu, Peștera Mică*) with fragmentary remains are not mapped.

Pre-Gravettian Modern Human Fossils from Western Central Europe

We have come to expect the fossil record of any region to constantly grow, but, in the case of early modern humans from western Central Europe, the opposite has happened. Presumed early specimens, such as those from Binshof-Speyer, Hahnöfersand, Vogelherd (Stetten), and Paderborn-Sande, have all been redated to the Holocene (with the last being less than 300 years old!) (Conard et al., 2004; Street and Terberger, 2002; Street et al., 2006; Terberger et al., 2001). Radiocarbon dates (Müller-Beck, 1983), as well as the numerous Aurignacian artifacts from the two strata from which the Vogelherd human remains were collected (Riek, 1934), had indicated that the remains dated to > 30 ka. However, recent direct AMS ^{14}C analyses yielded dates for the human remains that span from $3,560 \pm 30$ years ^{14}C BP for Stetten 2 to $5,175 \pm 30$ years ^{14}C BP for Stetten 3 (Conard et al., 2004). Thus, all of the Vogelherd human remains were from intrusive Neolithic burials that were not detected during excavation.

Although the incorrect and, until recently, accepted dates for the Vogelherd remains can be understood as the result of early and imprecise excavation, the incorrect dates for Binshof-Speyer, Hahnöfersand, and Paderborn-Sande (Table 5.1) have their origin in outright forgery (Harding, 2005; Pincock, 2005; Street et al., 2006). “Direct dates” for all three of these specimens were provided by the now-defunct Frankfurt University radiocarbon lab. As AMS dating was later applied to these specimens, it became apparent that the Frankfurt dates were consistently incorrect and gross overestimations (Street and Terberger, 2002, 2004; Street et al., 2006; Terberger et al., 2001). Kelsterbach, another specimen that was also given an early date by the Frankfurt laboratory, was used by Protsch as evidence for an early presence of modern humans in Central Europe (Protsch and Semmel, 1978). This specimen has gone missing and its date cannot be verified or, more likely, falsified by new dating (Street et al., 2006). We concur with Street and colleagues’ (2006) suggestion that Kelsterbach’s Aurignacian-age date be rejected as well.

So, what is left of the early modern human fossil record in western Central Europe? Unfortunately, none of the remaining candidates have been directly dated, and, even if we accept that these remains are Aurignacian, they are few and largely not diagnostic anatomically. Street and colleagues (2006) provide the following as “possibly Aurignacian Age” (p. 563; see also Table 3): a single premolar from Hohlenstein-Stadel, three teeth from Sirgenstein, two teeth from Schelklingen, a tooth from Kleine Ofnet, another tooth from Schafstall, and yet another single tooth from Geißenklösterle. They, furthermore, mention fragmentary remains from Honerthöhle as having a possible but uncertain association with Aurignacian artifacts. Thus, it is currently unclear what biological population was associated with the Aurignacian of western Central Europe.

The relative lack of early modern human remains from this region is ironic given the wealth of Aurignacian archaeological discoveries that have been made in the last couple of decades, especially in the Swabian Jura (Conard, 2009; Conard et al., 2009). The basal Aurignacian in this area may be as old as 40,000 years BP and has yielded the oldest undisputed bone and ivory flutes and a venus figurine from Hohle Fels (Conard, 2009; Conard et al., 2009). Additional, albeit more recent, Aurignacian flutes are known from Geißenklösterle (Hahn and Münzel, 1995) and Vogelherd (Conard and Malina, 2006). Recent work at Hohle Fels documents a significant technological shift across the Middle to Upper Paleolithic boundary, indicating, perhaps, a shift in human population as well (Conard and Bolus, 2008). Although Conard and colleagues (Conard, 2009; Conard et al., 2004) and others (Street et al., 2006) contend that the Aurignacian was likely brought into the Swabian Jura by invading modern humans, perhaps as the initial colonization of Central Europe by this population, the available evidence is insufficient to test such a hypothesis at this time.

Gravettian Modern Human Fossils from Western Central Europe

It is only in comparison with the Gravettian fossil record of western Central Europe that the region's Aurignacian fossil record looks rich. With the redating of the Binshof specimen to the Bronze Age (Terberger and Street, 2001), the Gravettian human fossil record of western Central Europe now comprises only two teeth from Geißenklösterle and a single tooth and cranial fragment from Hohle Fels. The Geißenklösterle teeth comprise a right upper deciduous molar and another deciduous molar (Haas, 1991; Hahn et al., 1990). The Hohle Fels Gravettian tooth is a right lower deciduous molar, while the cranial fragment may be from a young adult (Haas, 1991). As Street and colleagues (2006) point out, the paucity of Gravettian fossils in Germany contrasts with the number of documented Gravettian sites in the country as well as with the large Gravettian skeletal samples from Moravia. As is the case for the Aurignacian-associated remains from western Central Europe, the Gravettian remains are largely uninformative about the biology of the Gravettian peoples in this region.

Pre-Gravettian Modern Human Fossils from Eastern Central Europe

Although the eastern part of Central Europe has now traded places with the western part as the area with the most information about the biology of the first modern humans in the region, the record is far from perfect. The Mladeč fossils have played a role in understanding modern human origins in this region for some time, but the claim of unclear association with the Aurignacian, at least for some of the human fossils, and the lack of direct dates (but see Wild et al., 2005) have made their role, at times, tenuous. Questions still remain about the chronology and context of the Mladeč remains as well as how to interpret their mosaic anatomy. As in the case of the German Upper Paleolithic fossil record, direct AMS ^{14}C dating (Smith et al., 1999; Svoboda et al., 2002) has assailed the “early” status of three modern fossils that had featured prominently in earlier discussions (cf. Churchill and Smith, 2000; Smith, 1976a, 1982, 1984; Smith and Ranyard, 1980). The fragmentary remains from Svátý Prokop (Bohemia), the Velika Pečina frontal (Hrvatsko Zagorje), and the partial skeleton from Zlatý Kůn (Bohemia) all succumbed to such redating (Table 5.1). While Zlatý Kůn remains (barely) Pleistocene in age following direct dating (Svoboda et al., 2002), the Svátý Prokop and Velika Pečina remains are now dated to the Holocene (Smith et al., 1999; Svoboda, 2005). Other remains¹³ that have been suggested as potentially early (cf. Churchill and Smith, 2000) have not been directly dated and have unclear or no associations with artifact industries. In the case of the Podbaba calvarium, direct dating will never be possible since the specimen was destroyed in 1921 (Churchill and Smith, 2000). Given the lessons of Velika Pečina, Zlatý Kůn, and the numerous German fossils discussed earlier, the Podbaba and Silická Brezova remains should not be included in discussions of early modern humans in Central Europe. The molar germ of Istállós-kő lacks a direct date, but its association with the Aurignacian may be more acceptable (Tillier et al., 2006) than the speculative dates for Podbaba and Silická Brezova. Yet its age should also be treated with caution.¹⁴

Despite more than 25 years, little still can be reported on some early modern human fossils that Smith (1984) was only able to describe briefly. For example, the Miesslingtal juvenile mandibular corpus remains undated but is reported to come from an Aurignacian context (Felgenhauer, 1950; Sombathy, 1950). Anatomically, Sombathy reports that it is modern human, and its dental metrics fall with the early Upper Paleolithic (Smith, 1984). The reportedly Aurignacian germ M_1 (Bailey et al., 2009) or M_2 (Malán, 1955; Tillier et al., 2006) from Istállós-kő lacks an anterior fovea and exhibits a buccolingual dimension closer to

Upper Paleolithic modern humans than to Neandertals. Nevertheless, Tillier and colleagues (2006) contend that no features of the tooth can distinguish it from Neandertals or modern humans. More recently, Bailey and colleagues (2009) note that the tooth lacks both a hypoconulid and a midtrigonid crest, aligning it with Upper Paleolithic modern humans. The three anterior teeth from the Aurignacian F_d stratum at Vindija Cave, as noted by Smith (1984), are large and anatomically fall with both Neandertals and early modern humans. An additional Aurignacian fossil, the Vi 302 left parietal fragment, was published by Smith and colleagues (1985). This specimen articulates with the previously unprovenanced Vi 204 right parietal. These conjoined pieces exhibit moderate lambdoidal flattening combined with greater biparietal expansion than that usually seen in Neandertals. Overall, the Vindija Aurignacian-associated remains are not diagnostic. Furthermore, given chronological uncertainties and lessons learned from directly dating other supposed early modern human fossils, the Miesslingtal, Istállós-kő, and Vindija F fossils should be only tentatively placed in the pre-Gravettian modern human sample until direct dates and/or additional chronological information become available.

Mladeč

The oldest directly dated, Aurignacian-associated modern human remains from Europe come from the Moravian site of Mladeč, a cave system located inside of Třesín Hill in the Czech Republic. The remains from this site, as well as possibly associated Upper Paleolithic artifacts, were not the result of habitation but rather were likely dropped through a vertical chimney (Svoboda, 2000, 2006). Excavations led by Szombathy in 1881–1882 uncovered numerous elements from the “Dome of the Dead” area of Chamber D in the Main Cave. These remains include the two, possibly female, crania Mladeč 1 and 2 as well as the Mladeč 8 maxilla, Mladeč 3 child, and several postcranial pieces. In 1904, the so-called “Quarry Cave” was accidentally discovered some 43 meters west of the Main Cave. Although many artifacts and bones were lost during and initially after the original discovery of this chamber, the possibly male crania, Mladeč 5 and 6 and other elements, as well as many artifacts, were recovered and curated (Frayner et al., 2006; Svoboda, 2006c). Additional human remains were found as late as 1922. Unfortunately, most of the at least 137 skeletal elements were lost in 1945 during the burning of Mikulov Castle, where the specimens discovered after Szombathy’s original excavations were stored. Only the Szombathy collections (at the Natural History Museum in Vienna), four hand bones and four cranial fragments from the private collection of Jan Knies, and Mladeč 5 remain, the last having survived the Mikulov fire.

The Mladeč remains, recognized as potentially early and associated with the Aurignacian, gained attention by the late 1970s. While Stringer (1974, 1978) viewed them as fully modern and lacking any Neandertal aspects, others (Frayner, 1986; Smith, 1984; Wolpoff, 1999) saw otherwise, especially in specific details of anatomy. This gulf in interpretation of the evolutionary significance of the Mladeč fossils persists with Bräuer (Bräuer and Broeg, 1998; Bräuer et al., 2006) reiterating Stringer’s interpretation while Frayer and colleagues (Frayner et al., 2006; Wolpoff et al., 2006), Churchill and Smith (2000), Cartmill and Smith (2009), and Trinkaus (2005, 2007) continue to argue in favor of the presence of Neandertal features among the Mladeč remains.

Confounding interpretations of the Mladeč fossils has been the difficulties in understanding their provenience, chronology, and archaeological associations (Frayner et al., 2006; Svoboda, 2006c). The fact that the more gracile, and presumably female, crania (1 and 2) and a large, likely male maxilla (Mladeč 8) came from Szombathy’s excavations of the Dome of the Dead in Chamber D, while the robust, presumably male, crania (5 and 6) came from

the adjacent Quarry Cave, questions whether or not all of the Mladeč fossils represent the same population and/or time period. Direct dating of Mladeč 1, 2, 8, 9 and 25c (proximal ulna), all from Chamber D, has helped tighten up the chronology for the Main Cave specimens, but the lack of direct dates for the only surviving Quarry specimen, Mladeč 5,¹⁵ does not help clarify the question of contemporaneity between the two samples. AMS ¹⁴C dating of Mladeč 1, 2, 8, and 9 (canine—white colored collagen) provide age estimates ranging from 30,680 to 31,500 radiocarbon years ago (Wild et al., 2005; Wild et al., 2006).¹⁶ Wild and colleagues (2006: 155–156) also note that these are uncalibrated ages and that “a shift of the ‘true ages’ by several thousand years towards higher ages might be possible.”

Lithic artifacts from Mladeč are rare and largely non-diagnostic, with only one distinctively Aurignacian carinated end scraper found (Oliva, 2006). There is, however, an extensive bone tool sample made up of numerous bone points (especially massive based/Mladeč points), awls, worked animal metacarpals (some with drilled holes), carnivore and beaver teeth with bored holes in the roots, and other items (Oliva, 2006). As noted by Oliva (2006), most of these bone artifacts derive from the Main Cave, but some were recovered in the Quarry Cave. This indicates the Quarry and Main Caves are roughly contemporaneous (see also Frayer et al., 2006). Oliva (2006) assigns the artifacts to middle to late Aurignacian.

The postcranial remains from Mladeč are basically modern (Trinkaus et al., 2006a). These remains are somewhat fragmentary and some are quite robust. Several features (e.g., cervical vertebral height, radial tuberosity position, shape of the proximal femora, talar trochlear size) overlap with the same features in Neandertals but also fall into the Skhül-Qafzeh early modern range from the Near East. Thus they are not conclusive evidence of a Neandertal contribution to the Mladeč people. Both femora exhibit the proximal-lateral femoral flange that tends to be found in European Neandertals and early moderns but not in the Near Eastern Neandertals and early moderns (Cartmill and Smith, 2009). This might be evidence of European continuity, but the polarity of this trait is not clear. One of the lost specimens, a proximal femur (Mladeč 78), shows strong anterior-posterior curvature, a trait common in Neandertals but not uncommon in early moderns.

The craniodental remains have traditionally been considered as showing the best evidence of continuity (Churchill and Smith, 2000; Frayer, 1986; Jelínek, 1969; Smith, 1982). The robust male crania (Mladeč 5 and 6) have been emphasized in this respect. In their recent analysis of the Mladeč males, Frayer and colleagues (2006) note that these are not Neandertals but that a hypothesis of equal ancestry from Neandertals on one hand and the Skhül-Qafzeh group on the other cannot be rejected (see also Wolpoff et al., 2001). Frayer and colleagues (2006) focus on overall shape of the vault (particularly the low vault height), parietal bone shape, the presence of occipital bunning and lambdoidal flattening, pronounced browridges, a projecting upper face (but with a pattern of flatness different from Neandertals), and an inferior bulging of the occipitomastoid region, resulting in relatively non-projecting mastoid processes, as particularly demonstrating continuity with European Neandertals. They also note the large tooth size, especially the canines of Mladeč 8 and 9, and the shoveling of the latter as further indicators. The possible female crania (Mladeč 1 and 2) are described as showing less evidence of continuity but still exhibiting occipital bunning and lambdoidal flattening (only present in Mladeč 1), and the same mastoid-occipitomastoid area morphology as the males (Wolpoff et al., 2006). The morphology of the Mladeč 3 child's skull (aged to >2 years) is described as being intermediate between Neandertal and modern human juvenile neurocrania (Minugh-Purvis et al., 2006). Medial browridge development, the prominent occipitomastoid area, lambdoidal flattening, and occipital bunning are all indicators of the specimen's intermediate status, while several other features are more clearly aligned to the modern human pattern. In summing up their views on Mladeč, Frayer and colleagues (2006: 266) note that “the exact details of the ancestry of

Mladeč may never be worked out”, but they interpret the data as supporting a minimum of 25–50% of Neandertal ancestry for the Mladeč people.

Not everyone accepts the Mladeč morphology as indicative of a Neandertal contribution to early modern Europeans. In a recent investigation of overall cranial form, Weber and colleagues (2006) compare the Mladeč 1, 5, and 6 neurocrania to a sample of anatomically modern humans and archaic humans, the latter consisting of Neandertals and earlier members of the genus *Homo*. The results of this analysis led them to conclude that the Mladeč crania “are clearly anatomically modern except the shapes of Mladeč 5 and 6 in the parieto-occipital region” (Weber et al., 2006: 465). They note more overlap in the morphology of this latter region in their analyses and conclude that overall posterior cranial form does not distinctly separate Neandertals and anatomically modern humans. Earlier Bräuer and Broeg (1998) argued that analysis of discrete cranial features does not show evidence of continuity, nor did a metric analysis of the fronto-facial region (Bräuer et al., 2006). Frayer and colleagues (2006) dispute the discrete trait study, but the other two studies underscore what earlier multivariate metric studies have generally found: the Mladeč crania have a basically modern form. This mirrors the conclusions based on the postcranial remains.

One feature that figures prominently in discussions of Mladeč and the issue of continuity is occipital bunning. Often it is suggested that the bunning in Neandertals and that in early modern Europeans was not homologous. It has long been recognized that the buns in early moderns were generally not as laterally extended as in Neandertals and were located relatively more inferiorly in the former (Smith, 1982; Cartmill and Smith, 2009). However two recent studies of bunning in Neandertals and early modern Europeans conclude that the structures are homologous (Gunz and Harvati, 2007, 2011; contra Nowaczewska and Kuzminski, 2009). The Harvati and Gunz studies conclude that the bunning morphology is a part of the integrated form of the cranium and should not be used as an independent trait to argue for European continuity. Of course, most everything in the cranium is integrated to some extent at least, but the fact is that European Neandertals and early moderns commonly exhibit a character state where the structure of a bun is specifically definable morphologically (Cartmill and Smith, 2009). Given this, it seems unreasonable to discount the definability of the feature. Interestingly, the external geometrical results presented by Weber and colleagues (2006: 465) found that this region of the Mladeč 5 and 6 crania was the only area in which they are not “clearly anatomically modern.”

Another occipital feature that figures prominently in the debate on Mladeč and the question of Neandertal–early modern European continuity is the suprainiac fossa (Figure 5.10). In Neandertals, this is a horizontally elongated, elliptical depression just above the superior nuchal line, normally identified by a grainy appearance of the external table in the depression. Frayer and colleagues (2006) maintain that Mladeč 6 is the only early modern European that has a Neandertal-like fossa, albeit weakly developed. Mladeč 5 has a small, circular depression with similar surface characteristics located at the midline just above the superior nuchal line. There has been considerable controversy concerning the relationship of the Neandertal suprainiac fossa to a variety of similar manifestations in early modern Europeans, including the two Mladeč variants (Ahern, 2006a; Balzeau and Rougier, 2010; Cartmill and Smith, 2009; Nowaczewska, 2011). It seems clear that some of the variants recognized as possible suprainiac fossae in the past represent something not homologous to the Neandertal feature, a fact first noted by Caspari (1991). The most convincing study is by Balzeau and Rougier (2010), who demonstrate a structural difference in the fossa of Neandertals and those of modern humans. Neandertal depressions are the result of diploic thinning, while the moderns’ result from external bone table thinning. If confirmed this would essentially remove the suprainiac fossa from the debate on continuity as the depression would be clearly non-homologous. One issue that needs to be addressed is that

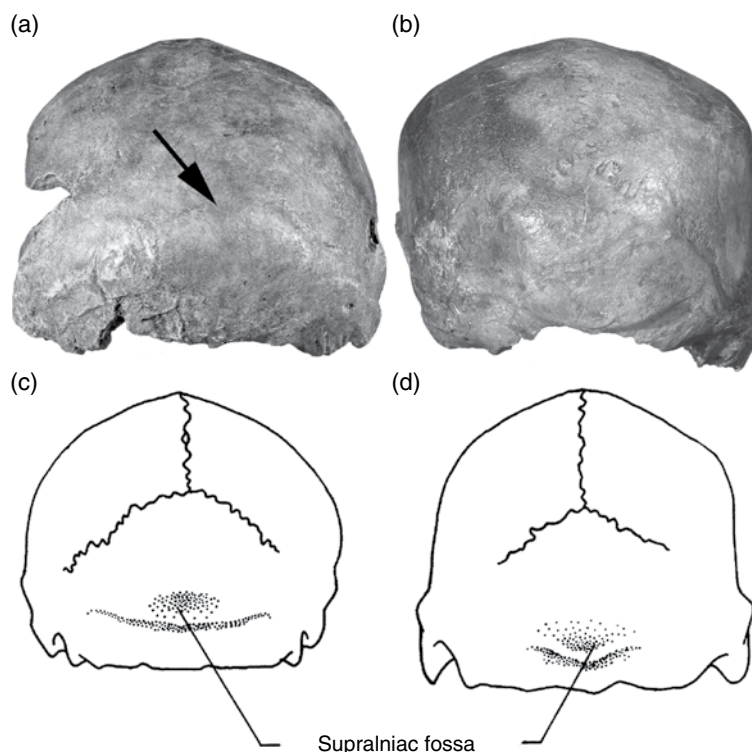


Figure 5.10. Mladeč 6 (a) and Mladeč 5 (b) in posterior view with a diagram, below, showing the (c) Neandertal-pattern and the (d) Upper Paleolithic modern-pattern suprainiac fossae. The arrow points to Mladeč 6's Neandertal-pattern suprainiac fossa. Mladeč 5 lacks a suprainiac fossa. Figure from Frayer et al. (2006). Photographs by Wolfgang Reichmann. Illustration by D. W. Frayer. Figure used courtesy of D. W. Frayer.

Balzeau and Rougier do not include any early Upper Paleolithic Europeans in their study. The fact that the structure might represent a functional adaptation (Caspari, 1991; Nowaczewska, 2011) would not necessarily remove the possibility of homology.

Peștera cu Oase

The site of Peștera cu Oase, located in southwestern Romania, was discovered during speleological exploration in 2002. A human mandible, Oase 1, was discovered at that time lying on the surface (Trinkaus et al., 2003b). Further exploration between 2003 and 2005 yielded most of a human cranium, Oase 2. Direct AMS ^{14}C dating of the Oase 1 mandible yielded dates of 35.2 ka ^{14}C BP (OxA-11711) and $34.29 \pm 0.97/-0.87$ ka ^{14}C BP (GrA-22810) (Trinkaus et al., 2003b). Attempts at dating the Oase 2 cranium yielded a minimum date of $28.89 \pm \infty/-0.17$ ka ^{14}C BP (Rougier et al., 2007), although Rougier and colleagues contend that Oase 2 may be contemporary with Oase 1. Unfortunately, there are no artifacts associated with the Oase remains.

The anatomy of the Oase 1 mandible (Figure 5.11) affiliates it with both later Upper Paleolithic humans as well as contemporary modern humans from elsewhere such as Nazlet Khater (Trinkaus et al., 2003b). Metrically, Trinkaus and colleagues' (2003b) discriminant function analysis (Neandertals vs. early Upper Paleolithic) places Oase 1 clearly among the early Upper Paleolithic specimens (posterior probability=0.994). In details of anatomy,



Figure 5.11. The Oase 1 mandible. Right lateral (a) and medial views of the (b) left and (c) right rami. Scale is in centimeters. Images courtesy of E. Trinkaus.

Oase 1 presents a chin but with only slight development of the mental tubercles and a fairly vertical symphyseal angle (Trinkaus et al., 2003b). It lacks a retromolar space and presents a mental foramen in line with the second premolar and a symmetrical mandibular incisure, all of which align it more with modern humans than Neandertals. Like the roughly contemporary North African specimen Nazlet Khater 2 as well as many Middle Pleistocene mandibles, but unlike those from the European Upper Paleolithic, Oase 1's ramus is especially broad. Given Oase 1's date and its anatomy, it is the oldest known anatomically modern human in Europe.

Nevertheless, two features of the Oase 1 mandible are specifically Neandertal-like. First, it exhibits a slight medial pterygoid tubercle as well as a horizontal-oval mandibular foramen pattern¹⁷ (Trinkaus et al., 2003b). The former is nearly ubiquitous among Neandertals and present among only 10% of early Upper Paleolithic specimens. The latter feature is found among 52.6% of Neandertals and 18% of early Upper Paleolithic (Cartmill and Smith, 2009; Frayer, 1992; but cf. Trinkaus et al., 2003b, for different but very similar frequencies). These are not features found among African or west Asian early modern humans, and their presence in Oase 1 suggests some Neandertal genetic contribution (Cartmill and Smith, 2009; Trinkaus et al., 2003b).

The Oase 2 cranium (Figure 5.12) exhibits a more intriguing morphological mosaic. It is unclear if this specimen is as old as the Oase 1 mandible, but the direct minimum radiocarbon



Figure 5.12. The Oase 2 cranium in anterior (a) and left (b) lateral views. Scale is 10 centimeters. Images courtesy of E. Trinkaus.

date (see above) certainly places it in the larger group of the oldest known European modern humans that includes those from Mladeč, Cioclovina, and Muijerri (Dobos et al., 2010; Rougier et al., 2007). The gestalt of the cranium places it clearly as a modern human. The vault is high, especially posteriorly. The zygomatics are large and the lateral cheeks are fairly anteriorly placed, unlike Neandertals. Oase 2 also exhibits well-excavated canine fossae, a fairly narrow nasal aperture, and a short face in comparison to Neandertals. In posterior view, Oase 2 exhibits the *en maison* form with vertical sides, contrasting with the *en bombe* form of most Neandertals. Metrically, Oase 2's vault is similar to that of Nazlet Khater 2 as well as other early modern humans (Rougier et al., 2007). The supraorbital region shows the modern pattern of separate medial and lateral segments divided by a supraorbital sulcus (Smith and Ranyard, 1980). Based upon wear on the first two molars combined with the presence of the third molars in their crypts (Rougier et al., 2007), Oase 2 was likely a late adolescent. Given that browridge morphology does not usually develop fully until the third decade of life in males (and, perhaps, even later in females) (Ahern, 1998), not too much should be made of Oase 2's relatively gracile supraorbital morphology.

Other aspects seem to align Oase 2 with Neandertals. Its flat frontal is similar in form to Neandertals (specifically Shanidar 1) and is similar to Cioclovina in this respect, according to Rougier and colleagues (2007). Oase 2 also exhibits a "hemibun" type of occipital bunning. Although debate still exists as to whether or not this morphology is homologous to Neandertal occipital bunning (see above), its presence in Oase 2 and as many as 60% of Upper Paleolithic specimens may align them with Neandertals. Perhaps more intriguingly, Oase 2 exhibits a prominent juxtamastoid eminence. Although this feature is not as large as in the majority of Neandertals, it is similar in size to a minority as well as Mladeč 2 and Qafzeh 3. Mladeč 1 and 5 exhibit large juxtamastoids similar to the usual Neandertal condition. Dentally, Oase 2 exhibits unusually large molars that are significantly larger than Neandertals and other early modern humans. Rougier and colleagues (2007) make special note of the order of size progression, in that Oase 2's first molar is smaller than its second and its second is smaller than its third. Such a pattern is not present among other early modern humans but is present in a minority of Neandertals (Rougier et al., 2007).

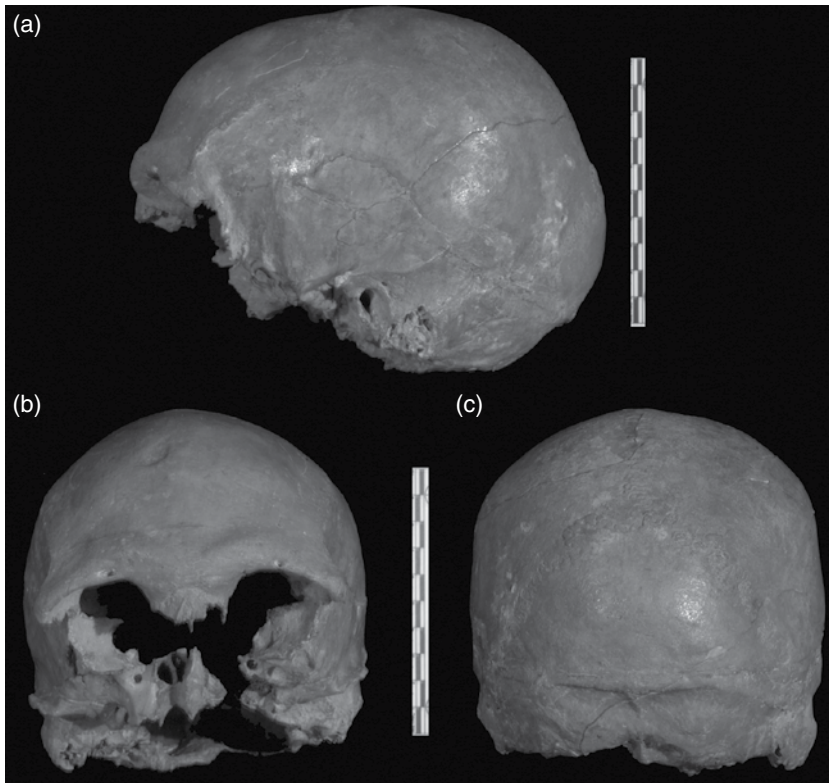


Figure 5.13. The Cioclovina cranium in left (a), anterior (b), and posterior (c) views. Images courtesy of E. Trinkaus.

Cioclovina and Peștera Muierii

In part because of the Oase discoveries, other early Romanian modern fossils have received renewed attention. Both the Cioclovina and Muierii fossil human remains have been known for more than a half-century, and specimens from both sites have recently been directly ^{14}C dated to 28.5–29.0 and 29.0–30.0 ka ^{14}C years BP (Dobos et al., 2010), respectively. This places both specimens among the earliest, securely dated modern human remains in Europe. Like Oase, however, neither specimen has firm archaeological associations. The Cioclovina 1 specimen is a probable male calvarium of uncertain associations and context found accidentally in 1940 or 1941 (Soficaru et al., 2006). Peștera Muierii has been known archaeologically since the late nineteenth century, and excavations in the early 1950s yielded a series of human remains associated with Middle Paleolithic tools in the back of one of the cave galleries (Galeria Musteriană) at the site (Dobos et al., 2010). Dobos and colleagues report that these remains were recognized as modern human, and thus their association with Middle Paleolithic artifacts was considered to result from artificial mixture in the cave. While there is also Upper Paleolithic at Muierii, it is not possible to establish the archaeological association of the human remains.

The Cioclovina 1 calvarium (Figure 5.13) is similar to the Mladeč (especially 1 and 2) and Oase crania in combining a basically modern form with some features potentially reflecting Neandertal influence. Soficaru and colleagues (2007) note the presence of a small hemibun,



Figure 5.14. The Muierii cranium in lateral view. Image courtesy of E. Trinkaus. Scale is 5 centimeters.

a suprainiac fossa, and other details of the occipital bone as examples of the latter group of features (see also Churchill and Smith, 2000; Smith, 1984). On the other hand, the form of the moderately robust browridge, the form of the mastoid process and occipitomastoid eminence, and other occipital features align the specimen with modern humans. This is also reflected in the form of the endocranial cast (Kranioti et al., 2011). Harvati and colleagues (2007) reaffirm the fundamental modern affinities of Cioclovina 1 and question the presence of possible Neandertal reminiscent features. However, they treat this specimen as a possible hybrid in their analysis, which would infer a greater amount of Neandertal influence than the previous studies would assert. Furthermore, most of their analysis compared overall cranial form using geometric morphometrics. All studies cited above agree that the overall cranial form is modern. The controversy over occipital bunning and suprainiac fossae discussed above is applicable also to the interpretation of Cioclovina 1.

The Pleistocene-aged human remains from Muierii comprise three individuals (Dobos et al., 2010): Muierii 1 (Figure 5.14)—a relatively gracile (likely female) cranium with the major portions of the neurocranial vault, a zygomatic bone and the maxillae, a right partial mandible, ten teeth (both maxillary and mandibular), a scapula and tibia; Muierii 2—a robust (likely male) left temporal bone; Muierii 3—a fibular fragment. Dobos and colleagues' (2010) description of Muierii 1 emphasizes the presence of several features that are derived for recent humans. Along with a high, rounded vault, these characteristics include a modern supraorbital region, infraorbital regions with distinct canine fossae, a high frontal profile, a small face with anteriorly positioned zygomatic roots, a narrow nasal aperture, and a modern dentition with extensive attrition. They also point out that Muierii 1 has a prominent occipital bun, an incipient development of a suprainiac fossa, and complete absence of an external occipital protuberance. These features are similar to those of

Cioclovina 1 and indicate possible evidence of a small Neandertal contribution to the population of which Muierii 1, Oase, and Cioclovina 1 are a part.

The same appears true for the Muierii 1 mandible, which preserves the lateral corpus from the P_3 alveolus to the ramus and most of the ramus. In keeping with the facial morphology of Muierii 1, the mandible is a small, gracile bone and indicates modern human levels of orthognathism. According to Dobos and colleagues (2010), the Muierii 1 mandible contrasts with those of most early modern humans in exhibiting features that suggest some affiliation with Neandertals. It has a high coronoid process with an asymmetrical mandibular notch. The anterior ramus lacks a distinct concavity. The mandibular notch crest does not meet the condyle clearly laterally. Dobos and colleagues do not see these as secondary reflections of spatial and/or biomechanical relationships within the face, particularly given the modern form of the Muierii 1 upper facial skeleton.

In the postcranium, Muierii 1 preserves a scapula with a bisulcate axillary border pattern (though trending toward a dominant dorsal sulcus) and a relatively narrow glenoid fossa, patterns that are found in other Upper Paleolithic specimens but also overlapping Neandertals and other archaic forms (Dobos et al., 2010). The Muierii 1 tibia and the Muierii 2 temporal are solidly modern human in form, but the Muierii 3 partial fibula is more archaic. Unfortunately, its context is uncertain, and it might derive from the Middle Paleolithic levels at the site.

As was the case for the Mladeč remains, the Romanian sample of Cioclovina, Muierii, and Oase represent a human sample that is immediately identifiable as modern. However, they also show individual features that likely reflect a small contribution of Neandertals. Interestingly, these tend to be found in the same anatomical regions in both samples, particularly the occipital (including the occipitomastoid eminence). The Romanian mandibular sample also exhibits some possibility of Neandertal contribution, but this is difficult to evaluate for Mladeč because the mandibles there were not carefully studied before their destruction.

La Adam, Bordu Mare, Peștera Mică, and Malu Roșu

Fragmentary fossils from four additional Romanian sites have been reported as deriving from Aurignacian contexts (see Table 5.4) (Alexandrescu et al., 2010). None of these fossils have published dates, much less direct ones.

Bacho Kiro

Eight human fossils were recovered from Aurignacian and “proto-Aurignacian” stratigraphic units at the cave site of Bacho Kiro, Bulgaria (Kozłowski, 1982). The oldest specimen, a left mandibular corpus preserving dm_1 (Bacho Kiro 1124), derives from stratigraphic level 11. Although originally dated to $>43,000$ ^{14}C years BP (Mook, 1982), four AMS radiocarbon dates from level 11 (Hedges et al., 1994) are all younger than the original date; they range from 33.8 ± 0.9 ka BP to 38.5 ± 1.7 ka BP. This time span for a single level may indicate a long period of accumulation, although contamination and/or level mixing may also apply (Hedges et al., 1994). The other Bacho Kiro specimens are associated with Aurignacian assemblages and derive from younger strata (6 and 7). They comprise five isolated teeth, a right parietal fragment, and a right mandibular corpus preserving dm_2 and M_1 (Churchill and Smith, 2000; Kozłowski, 1982). The dates for the level 6–7 material range from 32.7 ± 0.3 ka ^{14}C BP (Level 7/6b) to 29.15 ± 0.95 ka ^{14}C BP (level 6a/7) (Kozłowski, 1982). While Glen and Kaczanowski (1982) and Churchill and Smith (2000) found that the Bacho Kiro specimens fall, anatomically, in the area of overlap between Neandertals and Upper Paleolithic moderns, the latter concluded that the sample tended toward the Upper

Paleolithic modern human side of variation. Recently, Bailey and colleagues (2009), in their examination of a cast of one of the chronologically youngest Bacho Kiro Aurignacian specimens (#599 from Level 6a/7), tentatively concluded that it was most like Upper Paleolithic modern humans and not like Neandertals.

Görömby-Tapolca and Oblazowa

A robust but “fully modern” (Tillier et al., 2006: 99) occipital from Görömböly-Tapolca, Bükk Mountains, Hungary, was originally thought to be of Gravettian age (Tillier et al., 2006), but recent direct dating (30.3 ± 0.30 ka ^{14}C BP) places it earlier (Davies and Hedges, 2008–2009). A single distal thumb phalanx from the southern Polish site of Oblazowa has been directly dated to 31.0 ± 0.55 ka ^{14}C BP (Hedges et al., 1996).

Gravettian Modern Human Fossils from Eastern Central Europe

Postdating the earliest modern fossils and earliest Upper Paleolithic in eastern Central Europe are numerous human remains from the Eastern Gravettian. Chronologically, these remains fall into two time periods. First, as represented by the majority of the human remains, is the Pavlovian (~25–30 ka), followed by the Willendorf-Kostienkian (~20–25 ka). The remains from Dolní Věstonice, Krems-Wachtberg, Pavlov, and Předmostí are all probably Pavlovian, while Brno-Franzouska, Grub/Kranawetberg, and Willendorf (I and II) derive from the later period. Most of the remains are from Moravia, while the others are from Austria. The sites form three spatial clusters (Figure 5.9): (1) Krems-Wachtberg and the Willendorf sites come from the Danube valley west of Vienna; (2) Brno-Franzouska, Dolní Věstonice, Pavlov, and Grub/Kranawetberg lie in southern Moravia/northeastern Austria; and (3) Předmostí lies the farthest to the northeast. Although robust and, in a few cases, exhibiting some Neandertal-esque features (Trinkaus, 2007), the Gravettian remains are decidedly anatomically modern.

As with the other samples and regions discussed in this chapter, direct dating of human remains has helped exclude some that were once thought to be Gravettian in age (Table 5.1). Most notably, Svitávka (Vlček, 1971) has been dated to $1,180 \pm 50$ ^{14}C BP (Svoboda et al., 2002). This specimen's morphological similarities to Brno 3 were used to support an Upper Paleolithic age. However, Brno 3, now lost, is itself of questionable age (Svoboda et al., 2002), and for that reason we do not include it in our discussion of the early modern material from Central Europe. The Balla subadult remains from Hungary were once thought to be Gravettian in age (Vögel and Waterbolk, 1972), but recent direct dating places them in the early Neolithic (Tillier et al., 2009). Other direct dates on presumed Gravettian fossils have yielded results consistent with this designation. A rib from Dolní Věstonice 35 yielded a date of 22.84 ± 0.2 ka ^{14}C BP (Svoboda et al., 2002; Trinkaus et al., 1999), while dating of Brno-Franzouska resulted in a date of 22.68 ± 0.21 ka ^{14}C BP (Pettitt and Trinkaus, 2000). The Willendorf-Kostienkian date for the former is probably due to contamination, since other dates and the archaeology from Dolní Věstonice I all indicate an earlier, Pavlovian, age (Svoboda et al., 2002; Trinkaus et al., 1999). Dates on associated charcoal for the Dolní Věstonice II and Pavlov remains date them to ~25–27 ka (Trinkaus and Svoboda, 2006).

Pavlovian Remains from Eastern Central Europe

Pavlovian human remains are known from Předmostí, Dolní Věstonice, and Pavlov in Moravia. Additionally, the three infant skeletons from Krems-Wachtberg in the Danube

valley west of Vienna also date to this earlier period of the Eastern Gravettian. Much of the Moravian material has been known since before the 1980s and, thus, has figured prominently in discussions of modern human origins (Smith, 1984; Trinkaus and Svoboda, 2006; Veleminská and Brůžek, 2008). The Předmostí remains were excavated periodically between 1884 and 1928. The fossils from the Dolní Věstonice I site were uncovered between 1925 and 1974, and the Pavlov remains in 1954 and 1957 (Holliday et al., 2006; Svoboda, 2006a). Continuing excavations at Dolní Věstonice (DV II locality) during the 1980s as well as the identification of numerous human teeth and bone fragments from the faunal remains during 1997–1998 (Holliday et al., 2006) yielded considerably more Pavlovian remains. Additionally, major analyses of the Dolní Věstonice and Pavlov fossils and reanalyses of the Předmostí remains in light of recently discovered documentation have been published during the past decade (Trinkaus and Svoboda, 2006; Veleminská and Brůžek, 2008). The single and double infant burials discovered during 2005–2006 at Krems-Wachtberg have been briefly described and are dated (26.58 ± 0.16 ka ^{14}C BP) to the Pavlovian period (Einwögerer, 2005; Einwögerer et al., 2006).

The remains of approximately thirty individuals were excavated at the site of Předmostí (Matiegka, 1934–1938; Veleminská and Brůžek, 2008). Although most of the remains were once thought to have come from a mass or communal grave (cf. Smith, 1984), recent work has shown that the Předmostí “cemetery” resulted from consecutive interments of remains over a long period of time (Brůžek and Veleminská, 2008; Svoboda, 2008). The time span was long enough that it is possible that a small minority of the Předmostí remains may date from the later Willendorf-Kostienkian phase of the Gravettian (Svoboda, 2008). As in the case of Mladeč, most of the Předmostí remains were destroyed in the Mikulov fire at the end of World War II. However, two mandibular fragments, Předmostí 21 and 26, survived and have been described and analyzed in recent years (Drozdová, 2001; Vlček, 2008). Předmostí 21 preserves the premolars and molars from the right side and exhibits the sort of artificial buccal wear (Drozdová, 2001) seen in many other Gravettian teeth (Hillson, 2006; Teschler-Nicola et al., 2004; Trefný, 2008). Vlček’s (2008) brief description of Předmostí 26 does not report any similar artificial wear.

Veleminská and colleagues (see works in Veleminská and Brůžek, 2008) undertook a reappraisal of the Předmostí evidence based largely on Matiegka’s glass negatives and notes, as well as excavation notes left by K. J. Maška. The results of the works in the Veleminská and Brůžek volume (2008) largely confirm Matiegka’s (1934–1938) results and conclusions. Yet the reviews of the Matiegka and Maška documents fail to clarify the exact number of individuals as well as many of the bone associations. Seemingly, the only postcranial-cranial associations that are assured are for Předmostí 3 and Předmostí 4 (Frayser and Wolpoff, 2008).

To the southwest of Předmostí lie the adjacent sites of Dolní Věstonice and Pavlov (Figure 5.9). Although most of the remains from these sites were known prior to Smith’s (1984) review, the significant DV 13–15 triple and DV 16 single burials were discovered during the late 1980s (Holliday et al., 2006). DV 13 and 15 were in their early 20s at death, while DV 14 was slightly younger (Hillson et al., 2006). All three appear to be males, although some congenital abnormalities resulted in DV 15 appearing more female than normal (Brůžek et al., 2006). The male skeleton DV 16 was at least 45 years old at death, making it the oldest of all known Pavlovian individuals (Hillson et al., 2006). Evolutionarily, the anatomy of the DV 13–16 individuals largely confirms what was seen in the previously known Dolní Věstonice sample, although DV 16 is somewhat notable for its robusticity and archaic appearance (Franciscus and Vlček, 2006). At least one Neandertal-like characteristic of DV 16, its inflated infraorbital region, Franciscus and Vlček (2006) contend is due to postmortem change and/or congenital deformation. Furthermore, some degree of DV 16’s

robusticity may be due to its more advanced age at death compared to other Pavlovian remains, as some aspects of cranial robusticity development continue during adulthood (Ahern, 1998; Behrems, 1985; Enlow and Hans, 1996; Israel, 1968, 1971, 1973, 1977).

Cranially, the Pavlovian peoples are clearly modern, with tall, gabled vaults, browridges divided into medial and lateral segments, narrow nasal apertures (except DV 13 and Pavlov 1), and excavated infraorbital regions. Metrically, they cluster with later Europeans (Franciscus and Vlček, 2006; Jantz and Owsley, 2003; Velemínská et al., 2008). Yet some details of anatomy of the Pavlovian remains are not especially similar to recent Europeans. Most of the male crania exhibit fairly large browridges, albeit of modern form with distinct medial and lateral segments. Although their vaults are taller than Neandertals and, at least some pre-Gravettian modern humans, they are shorter than most recent Europeans. Furthermore, the Gravettian crania exhibit greater prognathism than recent Europeans, reflecting larger average teeth. Many of the Pavlovian crania exhibit hemibuns (or even true occipital buns, according to Trinkaus, 2007) and suprainiac fossae, although the latter are medially restricted (not horizontally oval) and not particularly similar to Neandertals (Franciscus and Vlček, 2006). Mastoid processes are large, protrude well below the juxtamastoids, and lack anterior tubercles.

Postcranially, the Pavlovian remains are modern. The upper limbs are less robust than Neandertals but also less robust than many recent modern humans (Trinkaus, 2006). Trinkaus (2006) attributes this to having a more efficient tool kit than Neandertals as well as lacking the rigors of agricultural life.¹⁸ Limb proportions and stature of the Pavlovian humans, as well as those of many other Upper Paleolithic moderns, are different from the earlier Neandertals and are more similar to those of the Skhül-Qafzeh peoples as well as recent sub-Saharan Africans (see Table 5.5). Holliday (2006) and others contend that the Gravettian limb proportions reflect a tropical climatic adaptation retained in recent migrants to glacial Europe. Countering this explanation, others have argued that the differences between Neandertals and the Gravettian limb proportions are mechanical ones (Caspari, 1992; Formicola, 1986; Frayer et al., 1993; Higgins and Ruff, 2011); that is, Neandertals were adapted for stronger quadriceps femoris reaction (Pearson, 1997), perhaps related to moving over rough, uneven terrain. While Holliday and Falsetti (1995) found no relationship between mobility and lower limb length among recent foraging populations (see also Weaver and Steudel-Numbers, 2005), Higgins and Ruff's (2011) analysis supports the contention that Neandertal lower limb anatomy was advantageous on sloped terrain.

Willendorf-Kostienkian Remains from Eastern Central Europe

Some of the Předmostí remains may have been Willendorf-Kostienkian in age, although we will likely never know if this was the case, much less which specimens were of this time period. The Willendorf-Kostienkian-age direct date from Dolní Věstonice 35 is probably due to contamination by younger carbon (Svoboda et al., 2002; Trinkaus et al., 1999). Of almost certain Willendorf-Kostienkian age are the human remains from Brno-Franzcouska, Willendorf (I and II), and Grub/Kranawetberg. The Brno-Franzcouska burial (Brno 2) was excavated in 1891. Its mode of burial, with numerous grave goods and covered by mammoth tusks, is consistent with a Gravettian classification. Furthermore, direct dating of the specimen confirms this (Pettitt and Trinkaus, 2000).

In Austria just up the Danube from Krems-Wachtberg, the Willendorf I and II sites have yielded two fragmentary fossils dating to the Willendorf-Kostienkian phase of the Gravettian. Willendorf I (from Willendorf I) comprises a femoral diaphysis that exhibits a pronounced pilaster and *linea aspera* as well as robustness that falls in the middle of the Upper Paleolithic range (Teschler-Nicola and Trinkaus, 2001). It has been directly AMS

Table 5.5. Limb proportions in the eastern Central European Gravettian and comparative samples.¹

	Brachial Index	Crural Index
Eastern Central European Gravettian		
Dolní Vestonice 3	76.7	86.0
Dolní Vestonice 13	77.1	86.6
Dolní Vestonice 14	76.2	82.5
Dolní Vestonice 15	77.3	89.6
Dolní Vestonice 16	79.2	83.5
Pavlov I	75.7	
Předmostí 3	77.2	86.5
Předmostí 4	78.1	87.1
Předmostí 9 ²	78.7	79.4
Předmostí 10 ²	78.5	85.1
Předmostí 14 ²	79.1	87.0
Average	77.6	85.3
(s, n)	(1.2, 11)	(2.9, 10)
W. Asian Neandertal	78	77
(s, n)	(2.4, 5)	(2, 5)
Qafzeh-Skhul	76.5	83.7
(s, n)	(5.5, 3)	(5.9, 2)
Recent Europeans	75.0	82.7
(s, n)	(2.5, 391)	(2.4, 436)
Recent sub-Saharan Africans	78.6	85.3
(s, n)	(2.8, 152)	(2.4, 158)
European Neandertals	73.2	78.7
(s, n)	(2.5, 5)	(1.6, 4)
All European Gravettian	77.7	85.1
(s, n)	(2.0, 20)	(1.8, 18)

¹Data from Holliday (1995, 2006) and courtesy of M.H. Wolpoff.

²The postcranial associations for these specimens are not certain (Fraye & Wolpoff, 2008).

radiocarbon dated to 24.25 ± 0.18 ka ¹⁴C BP (Teschler-Nicola and Trinkaus, 2001). Willendorf 2 (from Willendorf II) is a mandibular symphysis whose anatomy is similar to other early Upper Paleolithic mandibles. Although a *planum alveolare*, inferior lingual torus, and “indistinct” lateral mental tubercles are somewhat archaic features, the specimen exhibits a clear mental trigone, *fossa mentalis*, and other aspects of modern chin development (Teschler-Nicola and Trinkaus, 2001). Willendorf 2 derives from layer 9, which is approximately 23.9–24 ka BP.

At the site of Grub/Kranawetberg, two deciduous tooth fragments were discovered in 1996 and 1998 from Gravettian deposits dated to 24,400–25,500 BP (Antl-Weiser, 1999; Antl-Weiser and Teschler-Nicola, 2000/2001). One is a right first dm₁ (Grub/Kranawetberg 1: GK 96/634) and the other a left di² (Grub/Kranawetberg 2: GK 98/4028)

(Teschler-Nicola et al., 2004). According to Teschler-Nicola and colleagues (2004), both could have belonged to the same individual. The molar shows artificial buccal wear like other Gravettian teeth (see above; Hillson, 2006; Trefný, 2008). Metrically, the incisor is small compared to the few other Gravettian di²s. Although the small mesiodistal measure (5.1 mm) could be explained as due to interproximal and occlusal wear, the especially small buccolingual dimension (4.5) cannot. Nevertheless, comparative sample sizes preclude any significance to Grub/Kranawetberg 2's small dimensions (Teschler-Nicola et al., 2004).

Discussion

Our understanding of the evolutionary origins of modern humans in Central Europe and elsewhere has significantly matured since the middle of the nineteenth century. In the last twenty-nine years since Smith's 1984 review of the Central European evidence, there have been considerable advances, both in terms of evidence and theory. At the evidentiary level, new fossil discoveries (in particular the Oase and post-1984 Vindija specimens) have been important. However, the most dramatically new evidence has come from the application of new techniques to old fossils. In particular new dating methods and genomic analyses have transformed our available dataset. At the theoretical level, the debate has shifted from a relatively polarized one positing complete replacement of archaic Eurasians versus overall regional continuity to a discussion of how much admixture and its temporospatial pattern.

Evidentiary Level

Improved dating, especially the widespread application of direct AMS (including ultrafiltration) radiocarbon dating (cf. Higham et al., 2006; Jöris, 2011; Soficaru et al., 2007; Street et al., 2006; Wild et al., 2005, 2006), has provided a tighter chronology of the transition. For example, the direct dates for two of the Vindija G₁ specimens (Higham et al., 2006; Smith et al., 1999) as well as of the Oase (Trinkaus et al., 2003b) and Mladeč (Wild et al., 2005) remains have established that Neandertals and modern humans in eastern Central Europe were penecontemporaries. The incredible trimming of the early Upper Paleolithic human fossil record by the application of direct dating techniques, especially in the case of western Central Europe, has highlighted how little we know about the first modern humans in this area. The gracile, recent-European anatomy of Binshof-Speyer, Vogelherd (Stetten), and Paderborn-Sande remains all seemed to support a complete replacement of Neandertals, while the more robust Hahnöfersand frontal was used by Bräuer (1980) and others (e.g., Smith, 1984) as evidence of Neandertal-modern admixture. Direct AMS dating of these to the Holocene now makes them irrelevant for understanding modern human origins (Table 5.1). In addition to direct dating of fossils, further explorations of many sites have led to improved understandings of fossils' ages. For example, the new OIS 5e age for the Ša'la fossils makes them too early to be "transitional," as had once been argued (Smith, 1982).

Over the last 30 years, the genetics and genomics revolution has helped shape our understanding about modern human origins. For many years, starting with the mtDNA analysis by Cann et al. (1987), an exclusively African origin for all modern humans seemed likely (Stringer and Andrews, 1988). However, some (cf. Harpending and Eswaran, 2005; Harpending and Rogers, 2000; Relethford, 2001a,b,c and references therein) suggested different explanations were possible, and several studies have shown a considerable depth for some non-African genetic polymorphisms (Eswaran et al., 2005; Harding, 1997, 2000; Harding et al., 1997; Templeton, 2002, 2005; Yu et al., 2001), as well as some archaic non-African contributions to the modern human gene pool (Evans et al., 2006).

Likewise, analyses of mtDNA isolated directly from Neandertal specimens have added another dimension to the debate (Caramelli et al., 2006; Krings et al., 1997, 2000; Lalueza Fox et al., 2005, 2006; Orlando et al., 2006; Ovchinnikov et al., 2000; Schmitz et al., 2002; Serre et al., 2004). Although many interpreted the genetic evidence as supporting completely separate Neandertal and modern lineages (cf. Schwartz and Tattersall, 2010), developments in the field of ancient genomics illustrated that various processes (e.g., population expansions, migrations, bottlenecks, etc.) could cloud our insight into how past events affect modern human gene pools, and many haplotypes of mtDNA could have been lost over time (Adcock et al., 2001; Relethford, 2001a,b,c). What seems to emerge from all the ancient DNA studies is a low diversity of Neandertal mtDNA compared to living humans, suggesting a drastic bottleneck event. This must be taken into account in all explanatory models that use differences in genetic sequences as their datasets.

A new age for paleogenomics started with the successful extraction of nuclear DNA from one of the Vindija specimens (Vi 33.16) that previously yielded an mtDNA sequence similar to other Neandertal specimens (Serre et al., 2004). Interestingly, Green and colleagues (2006) show that the Vi 33.16 genome shares approximately 30% of SNP¹⁹ derived alleles with modern humans. This is best explained by gene flow between some Neandertal and early modern populations. More recently, Green and colleagues' (2010) analysis showing a 1–4% Neandertal contribution to living Eurasians provides further support of significant Neandertal-modern gene flow. Due to the aforementioned processes and the action of evolutionary mechanisms, this estimation must be seen as a minimum assessment. More recently, Sankararaman and colleagues (2012) report that the last gene flow from Neandertals into subsequent modern Europeans occurred 37,000–86,000 years ago. In short, current data do not support the distinction of Neandertals at a species level (Janković et al., 2011; Smith et al., 2005; Weiss and Smith, 2007).

Both mtDNA and the nuclear parts of the genome from recently found specimens from Denisova Cave in Siberia suggest more complex patterns of contact in various geographical areas (Krause, 2010; Reich et al., 2010, 2011). While Neandertal contribution, as noted above, is seen in contemporary Eurasians, the Denisovan contribution can be detected in present-day peoples of Melanesia. Although based on the DNA sequences it can be argued that the Denisovans are a sister group to Neandertals, caution is needed, as the reported bottleneck in Neandertals likely happened after the separation of their lineages (Reich et al., 2010) and thus limits our knowledge of Neandertal genetic variation.

Theoretical Level

Two models dominated the discussion of modern human origins from the late 1980s through the 1990s: (1) Out-of-Africa (Stringer, 1989), and (2) Multiregional Evolution (Wolpoff et al., 1984). Trinkaus (2007) contends that both of these models, at least in their strict senses, are now untenable, given the wealth of fossil, genetic, and archaeological data. A complete replacement of Eurasian archaics is just as unlikely as a pattern of overall in situ regional continuity. The middle ground, where there was both an origin for modern humans in Africa as well as subsequent admixture with archaic populations, remains the only viable explanation, according to Trinkaus (2007). Various models occupy this middle ground with the most prominent one being the Assimilation Model (Smith et al., 1989; Smith et al., 2005). However, it should be noted that various proponents of the two older and polarized models (Out-of-Africa and Multiregional Evolution) also have claimed this middle ground (cf. Cann, 1992; Caspari and Wolpoff, this volume; Hawks and Wolpoff, 2001a,b; Stringer, 1992; but see Smith et al., 2005). Hawks and Wolpoff (2001) argue that Multiregional Evolution has never required a worldwide pattern of overall regional continuity and that it

even allows for some local extinction of archaic populations. Stringer (1992), Cann (1992), and other out-of-Africa proponents (e.g., Bräuer, 1989) have stated that limited gene flow between modern humans and Eurasian archaics may have occurred but that this would not be inconsistent with the out-of-Africa model.

Models that encompass a wide range of possible admixture scenarios, such as Multiregional Evolution and Out-of-Africa, are useful for explaining the overall pattern of evolution of our species. However, such models, because of their breadth, may not be the most useful of explanations to test when it comes to understanding the temporospatial details of the origin of modern humans. These broad models may encompass the middle ground, but we must focus on testing more focused hypotheses in order to better understand these details.

The Evolution of Modern Humans and the Evidence from Central Europe

Few other regions have as much potential for understanding the details of modern human origins as Central Europe. We would like to bring the Central European record to bear on the examination of the following issues: (1) the problem of typology in understanding biology and culture across the transition, (2) the pattern of biological variation among Neandertals, (3) the appearance of modern humans and the disappearance of the last Neandertals, and (4) the degree and pattern of Neandertal and early modern human admixture.

Typology of Biology and Culture

A common thread to research on Neandertals since their first discovery has been an emphasis on demonstrating the distinctiveness of Neandertals from modern humans. Early on this was often used to demonstrate that Neandertals were not just another extinct race of humanity or pathologically deviant modern humans, but were, in fact, human ancestors (King, 1864; Schaaffhausen, 1857). By the early twentieth century, the motivation for making Neandertals distinct had shifted from seeing them as primitive ancestors of humans to being a fundamentally distinct and extinct branch on the family tree (Boule, 1921). Despite Brace's (1964) attack on this "pre-sapiens" perspective as typological and non-evolutionary, followed by the dismissal of the supposed fossil record of "pre-sapiens" (Trinkaus and Shipman, 1992), accepting Neandertals as an extinct side branch of our evolution continues to promote seeing them as different *in type* from ourselves. Numerous recent studies appear to begin with the assumption of distinctiveness and then demonstrate it (cf. Benazzi et al., 2011; Harvati et al., 2004; Ponce de Léon and Zollikofer, 2006; Tattersall and Schwartz, 2006). The revolution of geometric morphometrics, although an important methodological step forward, has been repeatedly used within a typological framework that emphasizes Neandertal-modern separation. Such a typology, as with all typologies, works well when our focus is away from the area of transition between two categories. Thus, as long as we continue to compare samples of mostly pre-OIS 3 Neandertals with mostly post-Aurignacian modern humans (cf. Benazzi et al., 2011; Harvati et al., 2004; but see Ahern et al., 2005), "Neandertal" and "modern" will appear to be distinct types. Furthermore, most of the well-preserved fossils of Neandertals come from the end of their range, Western Europe, which was farthest from their contemporaries. Thus, focusing on these well-preserved specimens to the exclusion of the fragmentary but numerous fossils from other regions, such as Central Europe, has helped further the Neandertal versus modern human typology. Yet, when it comes to understanding the process of the origin of modern humans in Western Eurasia, we

must focus, at least in part, on the period of the transition. Variation has the potential to be continuous across transitions. Thus, a typological perspective can potentially make us miss, or at least misunderstand, the very evolutionary process that interests us.

Categories like Middle or Upper Paleolithic are no less problematic and should be considered just general terms of convenience, not necessarily reflecting the reality of processes at various regions and at different times (indeed, not even in the same time). Growing archaeological data over the last hundred or more years have shown that the elegant schemes in which there is a clean break between these two periods of early prehistory do not really reflect reality (see Clark, 2009). Thus numerous scholars talk about so-called “transitional industries” that can be recognized within Europe (and elsewhere) between roughly 30 and 50 ka. As Straus (2009) rightfully notes, the problem lies in the emphasis on “transition” between two distinct entities, the Middle and the Upper Paleolithic, as this taxonomy implies there is a real and sharp break and change. However, it also implies that it stands between two other entities (in this case the Middle and the Upper Paleolithic) that are static in nature. This cannot be further from the truth. Many of the aspects and traits commonly associated with the Upper Paleolithic, like the use of blade technology, even prismatic blade technology, bone tools, non-utilitarian objects, and so forth, are found in various earlier contexts (i.e., Middle Paleolithic) (Straus, 2009). They may not be as common as in the Upper Paleolithic, but are there, and therefore one cannot easily define the abrupt change and breakup with earlier traditions. If one wants to find a sharper break, it is seen during the last glacial maximum and within the later phases of the Upper Paleolithic, not at the “Middle” to “Upper” Paleolithic transition. One additional problem with the term “transitional industries” is that most scholars try to ascribe it to biological groups (i.e., Neandertals or anatomically modern humans). It is accepted that Neandertals in Europe were responsible for the Middle Paleolithic, while the classical industries of the Upper Paleolithic were produced by anatomically modern newcomers (albeit in Western Asia this is not so and both groups are associated with Middle Paleolithic, Mousterian tools). Thus the same approach is applied to these “transitional” industries that are either attributed to late Neandertal groups or to the first anatomically modern humans in the region (see Adams, 2009; Chabai, 2003; Hoffecker, 2011 and references therein). Furthermore, the explanations for their appearance range from independent inventions (see Zilhão and d’Errico, 2003; Zilhão et al., 2006) by local Neandertals, to “acculturation” that came from the “moderns” (Harrold, 1989; Mellars, 1996; Mellars, 2006). This may have been a useful model, or models, to think about and test, but too much time and energy has gone into trying to fit the data into the preferred explanation. Harrold (2009) puts the “transition debate” in a historical context, outlining some of the major problems (see also Riel-Salvatore, 2009).

Realizing the conceptual problem, in recent years numerous authors have been trying to find novel and more productive ways of thinking about this “transition” (Brantingham et al., 2004; Clark, 2009; Peresani, 2011; Soffer, 2009; Straus, 2009 and references therein). Neandertals were very variable in time and space and in behavior as well as in biology. They successfully adapted to local needs and environments and used the available resources. The almost lack of specialization compared to later humans of the (later) Upper Paleolithic more likely was due to lower population density and different ways of life and resource use. Smaller groups did not need to waste their time and energy in massive game hunting. As Brantingham and colleagues (2004) note, the presence of a specific behavior or behavioral system is not necessarily an accurate predictor of biological phylogeny. We need to turn to site-by-site analysis. As Straus (2009) points out, there were many “transitions” at different times and places, at different rates and for different reasons. When approaching a specific assemblage, we must keep in mind we are dealing with a single site and that the cultural remains first and foremost reflect a specific function or activity, and so forth, and are not

representative of the industry, or culture, as a whole. Most were accumulated as a result of short occupation episodes by smaller groups and were not long-term dwelling places of the whole population. An even worse mistake would be making generalizations about the biology, taxonomy, and phylogeny of people responsible for these archaeological (*sensu stricto*) assemblages, when in the vast majority of cases, no human remains were found in association with them (and even when they are, there is not clear authorship).

The so-called “transitional industries” include the Châtelperronian of France and northern Spain, Szeletian and Jankovichian of central and parts of eastern Europe, Uluzzian of Italy (Tuscany, Calabria, southern Adriatic area, Uluzzo Bay, etc), Streletskian of eastern Europe, Jerzmanowician of eastern Germany and Poland, Althmülian of southern Germany, Bohunician of the Czech Republic, Brynzeny and Kostenki Szeletian of Russia, and several other unnamed or site-specific assemblages from Poland, Slovakia, the Czech Republic, Romania, and so on, in which various elements of the Mousterian (or Middle Paleolithic) appear alongside the Upper Palaeolithic types or types produced using technology commonly associated with the Upper Palaeolithic. Many scholars recognize the origin of these industries in local Mousterian variants and see no abrupt change (Allsworth-Jones, 1990; Anikovich, 1992; Bordes, 1972; Cabrera Valdés et al., 1997; Churchill and Smith, 2000; Clark and Lindly, 1989; D’Errico and Zilhão, 1998; Gioia, 1988; Golovanova and Doronichev, 2003; Harrold, 1989; Kozłowski, 2004; Kozłowski and Kozłowski, 1979; Laplace, 1966; Otte, 1990; Palma di Cesnola, 1993; Pradel et al., 1966; Rigaud, 1989, 1997; Straus, 1997; Svoboda, 1993, 2004; Valoch, 1972). In a recent study of the Uluzzian, Riel-Salvatore (2010) suggests this industry was restricted to the southernmost part of peninsular Italy. According to this author, the Mousterian is rather distinct from the Uluzzian *sensu stricto*²⁰ but also from other contemporary early Upper Paleolithic industries (proto-Aurignacian). However, the question of whether late Neandertals or early anatomically modern humans were responsible for this industry is unclear (see Benazzi et al., 2011; Churchill and Smith, 2000; Riel-Salvatore, 2009; Riel-Salvatore et al., 2012). Indeed, it might have been a population encompassing biological elements from both groups. Except for documented associations of Neandertal remains and Châtelperronian artifacts from La Roche à Pierrot at St. Césaire and Grotte du Renne at Arcy-sur-Cure (Hedges et al., 1994; Hublin et al., 1996; Leroi-Gourhan, 1958; Léveque and Vandermeersch, 1980; but see Bar-Yosef and Bordes, 2010; Higham et al., 2010), as well as the likely association of Neandertal remains with a “transitional” assemblage in level G₁ at Vindija (Janković et al., 2011), there are no diagnostic hominin fossils associated with any of these earliest Upper Palaeolithic finds (see Churchill and Smith, 2000).

These industries are either contemporary with, or, in most cases, earlier than the Aurignacian, the industry seen by most as the handiwork of anatomically modern humans as they move into the region (Bailey et al., 2009; Mellars, 1996, 2006), although some authors argue for local origins (see Oliva, 1993; cf. Bar-Yosef, 2006). An additional problem is that the Aurignacian is often regarded as a single imported complex that can be recognized in the archaeological record by the appearance of certain tool types and automatically assigned to anatomically modern populations. However, more and more studies show that several tool types (especially bone tools) used as indicative of the Aurignacian are in fact commonly found in various aforementioned “transitional” industries (Allsworth-Jones, 1990; Janković et al., 2006, 2011; Miracle, 1998; Svoboda, 1993, 2004, 2006b; Valoch, 1972). Furthermore, the Early Aurignacian differs from the Late Aurignacian (Miracle, 1998). Finally, there are great differences between assemblages of the typical Aurignacian from Western Europe, and that of Central/Eastern Europe (Karvanić and Smith, 1998; Miracle, 1998; Oliva, 1993; Svoboda, 2004). All this makes it clear that there may be a different pattern of behavioral and most likely populational change in Western vs. Central/Eastern Europe

(Janković et al., 2006, 2011). Kozłowski (2004) recognizes several differences between these “transitional” industries according to the source from which they derived.²¹ The industries that are characterized by the presence of backed points/blades, such as Châtelperronian, Uluzzian, and several site-specific industries in Poland, Slovakia, Moldova, and Romania, have no identifiable substrate and are quite widespread geographically. According to Kozłowski (2004), they arose independently of “Aurignacian” influence.

Biological Variation

Neandertal and adjacent populations’ biological variation across space and time can be informative about the patterns of selection, gene flow, and genetic drift. Under a scenario where Neandertals were completely isolated from adjacent humans until some very limited hybridization with invading modern humans (cf. Currat and Excoffier, 2011), we would expect the pattern of biological variation within Neandertals to be independent of the biology of adjacent populations. In other words, there should not be a west to east cline of Neandertal features with Western European fossils exhibiting the highest frequency of Neandertal features and with an increase of more modern features as one moves farther to the east. Furthermore, Neandertals should not accumulate more and more modern features over time, if they had been completely isolated.

Heterogeneity within Neandertal populations is well known in terms of morphology as well as ancient DNA (i.e., Degioanni et al., 2011; Fabre et al., 2009; Hambücker, 1998; Vandermeersch and Garraalda, 2011; Voisin, 2004). However, a more detailed approach to Neandertal morphology shows that more than being heterogeneous, their morphology displays a west to east cline (Voisin, 2006). Neandertals from Western Europe present more pronounced characters than Neandertals from the Near East.²² Recent works on the shoulder are consistent with this hypothesis (Di Vincenzo et al., 2012; Voisin, 2011). In other words, Western Neandertals could be viewed as “hyper-Neandertal” and Eastern ones could be viewed as “hypo-Neandertal.” Moreover, modern humans from Central Europe (as well as from the Near East) display some Neandertal traits that do not exist in modern humans from Western Europe (Voisin, 2006).

In terms of temporal variation within Neandertals, the case for Neandertals evolving in the direction of modern humans (cf. Smith, 1984; Smith et al., 1989) is less compelling than it once was. This explanation made sense when some more gracile and modern-like fossils were thought to be later in time than more “classic” or “hyper-Neandertal” fossils in the region. However, revised dating of some “transitional” fossils has moved them from being potentially late Neandertals to being much earlier (e.g., Ša’la, see Sládek et al., 2002). Furthermore, one of the most “classic” or “hyper-Neandertal” specimens from Central Europe, Feldhofer 1, has been dated to be quite late (Schmitz et al., 2002). Finally, the Hahnöfersand frontal’s new Holocene date (Terberger et al., 2001) has made its robust morphology irrelevant for understanding Neandertal–early modern human admixture. What remains, however, is the temporal sequence formed by the Krapina and Vindija samples. This sequence formed the core of past arguments about temporal change in Central European Neandertals (Smith, 1982, 1984; Smith and Ranyard, 1980; Wolpoff, 1980) with such specimens as Ša’la 1 used to illustrate that the temporal pattern was likely region-wide. As was the case then, fossil sample sizes remain small aside from those from Krapina and Vindija. So, although the Krapina-Vindija sequence hints at a localized temporal change in Central European Neandertals in the direction of modern humans, it does not demonstrate it.

The current evidence regarding temporospatial variation in Central European Neandertals is inconsistent with a scenario whereby Neandertals were fully isolated from extra-European populations, although such a scenario is not clearly falsified. A more conclusive testing of

this hypothesis must await more fossils or, at least, improved techniques for analyzing temporospatial variation when samples are very small and not randomly distributed through space and time.

Appearance of Modern Humans and the Disappearance of Neandertals

The oldest, directly dated fossil in Central Europe that exhibits sufficient modern features to not be called a Neandertal is the Oase 1 mandible, dating to $34.3 \pm 1.0/-0.9$ ka ^{14}C BP (Figure 5.2; Trinkaus et al., 2003b). The Oase 2 specimen yielded a date of > 28.9 ka ^{14}C BP. Recent direct dates of the Muierii and Cioclovina specimens place them approximately 4,000–5,000 years younger than Oase 1. All of the early Romanian fossil dates reported here used ultrafiltration pretreatment, which offers greater accuracy over standard AMS dating (Bronk Ramsey et al., 2004). Unfortunately, other early modern human remains from Central Europe have not been directly dated yet using this improved technique. The Mladeč Chamber D remains have been directly dated to 30.7–31.5 ka ^{14}C BP, but these dates are not ultrafiltration ones and thus may not be comparable to the Romanian dates. Nevertheless, it appears that anatomically modern humans are present in eastern Central Europe by ~ 30 –35 ka ^{14}C BP.

Before the redating of numerous remains to the Holocene, the western Central European “early modern human” sample played an important role in interpretations of the appearance of modern humans in Europe (cf. Churchill and Smith, 2000; Conard and Bolus, 2003). The *kulturpumpe* model’s presumption, that the earliest Aurignacian = anatomically modern humans, was based, in large part, on the presumed > 30 ka age of the Vogelherd human remains (Conard and Bolus, 2003). At this point, only a few fragmentary remains from western Central Europe are still thought to be Aurignacian in age, and direct dates are not yet available for any of these. Because of their fragmentary nature and lack of direct dates, it is currently not possible to provide a reasonable estimate for the appearance of anatomically modern humans in western Central Europe.

Equally as important as the date of the appearance of modern humans is the date of the last Neandertals in Central Europe. The Vindija G₁ specimens Vi-207 and Vi-208 provide the youngest dates of any Neandertals in the region at 30.6–34.2 ka ^{14}C BP (Higham et al., 2006). In western Central Europe, the Kleine Feldhofer Grotte fossils appear to be the youngest (c. 38.6–41.1 ka ^{14}C BP; Schmitz et al., 2002). All of the other Neandertal fossils from western Central Europe have not been successfully directly dated. While approximate chronology is known for most of them (Table 5.2), none exists (beyond “Pleistocene”) for either the Untere Klause or Zeeland Ridges specimens. Those with approximate dates all appear to be > 46 ka.

So, based upon dates of available specimens, the oldest modern humans in eastern Central Europe are 30–35 ka ^{14}C BP. While the oldest date of appearance in western Central Europe is far less clear, it seems likely that at least some of the few Aurignacian-associated human fossils in this area date to ~ 28 –30 ka ^{14}C BP, if not slightly older. The last Neandertals in eastern Central Europe date to ~ 30 –34 ka ^{14}C BP and in western Central Europe to ~ 38 –41 ka ^{14}C BP. Because the focus of this paper is on biology, we have not made any estimates of appearance and disappearance based on the presence or absence of particular archaeological industries. Although such evidence is more common in the record than fossils, we caution against the typology of such industries, not to mention a priori equating any of them with a particular “type” of human.²³ Furthermore, none of the available dates, of fossils or otherwise, are likely to be the *actual* dates for either the appearance of modern humans or the disappearance of Neandertals in the region, since taphonomical biases make finding the actual oldest or actual youngest very improbable (Martin, 1993; Surovell and

Brantingham, 2007; Surovell et al., 2009). In reality, modern humans likely appeared in Central Europe perhaps as many as a few thousand years before the last Neandertals and a few thousand years later than what the fossil record currently indicates. Thus, although the period of overlap in the region appears to be ~4,000 years based on dated specimens, it was likely longer.

Neandertal-Modern Admixture

Available genomic information clearly demonstrates admixture between Neandertals and modern humans (Hawks, this volume), with approximately 1–4% of living Eurasian ancestry derived from Neandertals (Green et al., 2010). The resolution of this evidence is such that it is presently not possible to tell the details of temporospatial patterning of such admixture. Thus, fossil anatomy remains as the best source of such insights.

There is a continuum of possible degrees of admixture that could be reflected in the Central European fossil record. These range from a complete replacement of Neandertals in the region (i.e., no admixture) to a high level of gene flow between Neandertals and modern humans. There are two lines of evidence that we can draw upon to test hypotheses of admixture for the region. First is evidence of gene flow from modern humans to Neandertals. The presence of characteristically modern human features in the last Neandertals in the region would indicate such gene flow. This gene flow could have taken place before a migration of modern humans into Europe (via exchange of mates between adjacent populations without a major population movement), and/or it could have taken place following a migration of modern humans into the region. In the case of the former, modern features may be present in Neandertal fossils that predate the earliest appearance of modern humans. In the case of the latter, there should not be such evidence and modern features should be limited to Neandertal fossils that postdate the appearance of modern humans. However, given the difficulties in determining when modern humans actually appeared in Central Europe, knowing which Neandertal fossils predate and which postdate this event is far from straightforward. Second is evidence of gene flow from Neandertals into modern humans. The presence of characteristically Neandertal features in the earliest and post-Neandertal modern humans would be indicative of such gene flow. The admixture may have taken place in Central Europe or it may have taken place exclusively outside of the region before the modern human population entered.

In the case of the Central European record, the Vindija G₁ fossils are the only ones that clearly postdate the appearance of modern humans in the region. However, the closest penecontemporary modern human fossils are more than 400 km away (Oase), and the potentially younger Mladeč remains are more than 350 km distant. Thus, it is unclear if the Vindija G₁ Neandertals or their immediate ancestors would have had any contact with modern humans. Anatomically, the small, fragmentary G₁ sample does not exhibit any clearly modern features (Ahern et al., 2004; Janković et al., 2006, 2011; Smith and Ahern, 1994; Smith et al., 1985; Wolpoff et al., 1981). The lack of clearly modern features, however, cannot falsify a hypothesis of admixed ancestry for the last Neandertals in Central Europe. As discussed above, the larger Vindija G₃ sample does exhibit some modern-like features (Ahern et al., 2004; Janković et al., 2006, 2011; Smith and Ahern, 1994; Smith et al., 1985; Wolpoff et al., 1981). This sample, which dates to approximately 38–45.6 ¹⁴C ka, predates the oldest Central European modern human fossils, although this may be an artifact of sampling. So, although we contend that the modern-like features of the G₃ Neandertals are due to gene flow with modern humans, unfortunately we do not have the chronological resolution to determine whether this gene flow was before or after a modern human population migration into Europe.

Regarding evidence of gene flow from Neandertals into modern human populations, there are clearly Neandertal (or at least Neandertal-like) features present in the earliest modern humans as well as later populations (Cartmill and Smith, 2009; Frayer, 1992; Trinkaus, 2007; Wolpoff, 1999).²⁴ Although not ubiquitous among pre-Gravettian modern humans in Central Europe, their presence in this sample is in marked contrast with their absence in the earliest modern humans in Africa and their low frequency among the Skhül-Qafzeh Middle Paleolithic humans. Furthermore, Wolpoff and colleagues (2001) report a similar degree of difference between the Mladeč male crania and Neandertals and between the former and the Skhül-Qafzeh male crania. Although the homology of some of these traits has been debated (especially in the case of occipital morphology), the most parsimonious explanation of the presence of these Neandertal-like traits in the earliest Central European modern humans is admixture.²⁵

That some Neandertal traits, albeit at lower frequencies, even persist into Gravettian populations in Central Europe is telling, given that these peoples postdate the oldest known Central European modern human remains (Oase) by approximately 10,000 years and the youngest known Central European Neandertals (Vindija G₁) by approximately 6,000 years. As Trinkaus (2005, 2007) points out, such a time gap means that these remains are not nearly as informative about the pattern of modern human origins as the pre-Gravettian fossils. That the gestalt of the Central European Gravettian fossils is decidedly modern cannot be taken, *a priori*, as lack of genetic continuity between Neandertals and Upper Paleolithic modern Europeans. Even if the Gravettian fossils lacked any evidence of Neandertal ancestry, such evidence could not refute a hypothesis of Neandertal–early modern admixture/continuity. However, the fact that some Neandertal features persist in the Eastern Gravettian fossils speaks to at least some degree of admixture in their ancestry (Frayer, 1992; Trinkaus, 2007). The “tropical” limb proportions (Table 5.5) in this population may reflect an even more recent (than the first appearance of modern humans in Europe) migration from lower latitudes. Alternatively, it might reflect a shift in locomotor mechanics from earlier populations, including earlier Upper Paleolithic ones, for which we know little about limb proportions. What the Gravettian limb proportion evidence cannot tell us is that the *first* modern humans in Europe came from Africa.

Assimilation in the Late Pleistocene of Central Europe

As pointed out by Smith and colleagues (2005), the available evidence remains insufficient to falsify any but the most extreme of models of modern human origins. Nevertheless, we think that one explanation, the Assimilation Model (Smith et al., 1989, 2005), offers the best fit with the evidence from Central Europe. This model posits that modern morphology, as a complex, evolved first in East Africa, and that, as this modern population spread out, it admixed to varying degrees with indigenous archaic humans, such as Neandertals. Thus, the overall pattern of modern human origins should reflect this overwhelmingly African origin combined with the persistence of some regional features that characterized archaic populations outside of the modern human homeland (Cartmill and Smith, 2009; Smith et al., 2005). This explanation is consistent with the current genomic evidence, in that the vast majority of living human ancestry appears to have come out of Africa in the Pleistocene (Cann et al., 1987; Thomson et al., 2000; Underhill et al., 1997), but that there are some alleles outside of Africa that have deeper roots in these regions (cf. Hammer et al., 1998, 2011; Harding et al., 1997; Harris and Hey, 1999; Huang et al., 1998). Furthermore, the paleogenomic estimate of 1–4% of living Eurasian ancestry being from Neandertals (Green et al., 2010)²⁶ is also commensurate with the Assimilation Model. The “mostly Out-of-Africa” model, based in large

part on the genetic evidence (Relethford, 2001a; Rogers and Harpending, 1992; Rogers and Jorde, 1995; Templeton, 2002, 2005), is for the most part the same as the Assimilation Model. As mentioned previously, Multiregional Evolution does encompass, at least in recent renditions (Caspari and Wolpoff, this volume; Hawks and Wolpoff, 2001a; Wolpoff et al., 2004), the scenario proffered by the Assimilation Model. In this respect, Assimilation is a more specific explanation and one that we think best fits the available evidence.

The Assimilation Model does allow for a certain range of possible degrees and patterns of admixture and other processes as part of its explanation of modern human origins. Furthermore, these may vary from one location to the next, even if our present fossil record does not offer the resolution to see such variation. The current evidence does allow us to examine, to a certain degree, the patterns of variation over time and from region to region (see “Biological Variation” section, above). The temporal pattern seems to indicate an increase in more modern-like features among Neandertals over time, although much of this hinges on the Vindija level G₃ sample that may actually postdate contact with modern humans (Cartmill and Smith, 2009). Although the temporal pattern is not very clear, the spatial pattern appears to indicate a west to east cline of decreasing frequency of “hyper-Neandertal” features (Voisin, 2006). A potential implication of this clinal variation, which may be accommodated within the Assimilation Model, is that there was a gradient of inter-fertility between Neandertals and early modern humans across the Neandertal range. Admixture between the two human groups may have been possible in the eastern part of the Neandertal range, like West Asia. In Central Europe the interbreeding may still have been possible but less frequent. In the western area of the Neandertal range, hybridization may have been trivial or perhaps even impossible (Voisin, 2006).²⁷ Such a pattern of gene flow corresponds to a speciation by distance (Ridley, 2004).²⁸ Moreover, this hypothesis is consistent with recent simulations about Neandertal/modern human interactions (Barton et al., 2012). An alternative explanation of the clinal pattern, which also would be consistent with the Assimilation Model, is that of isolation by distance without complete reproductive isolation of even western Neandertals upon a modern human spread into Europe. Although somewhat less frequent than in Central Europe, Neandertal-like features persist in early modern human fossils in Western Europe, as well (Trinkaus, 2007). One possible explanation for the Les Rois pre-Gravettian human sample from France is that it represents a hybrid population (Ramirez Rozzi et al., 2009). Also, certain aspects of the Gravettian Lagar Velho (Portugal) child’s anatomy appear to reflect some Neandertal ancestry, as well (Duarte et al., 1999; Zilhão and Trinkaus, 2002; but see Tattersall and Schwartz, 1999). However, the presence of Neandertal features among early modern humans in Western Europe, or Central Europe for that matter, does not necessarily mean that the modern population admixed with Neandertal of the same region, as their ancestors could have interbred with Neandertals in other regions before arriving.

Summary and Conclusions

New fossils, new dates, and new analytical techniques, over the last few decades, have improved our understanding of modern human origins dramatically. While many of these discoveries have been made regarding other regions, many have also been made about Central Europe. Most of the new Neandertal fossils from Central Europe are fragmentary and have not greatly changed our interpretations. However, the ~30–35 ¹⁴C ka BP Oase early modern human remains, with their Neandertal-reminiscent features, in combination with the dismissal-by-direct-dating of almost all of the gracile, “hyper-modern” human remains from the early modern European sample, have fundamentally changed our understanding

of the earliest modern humans and their admixed ancestry. New analyses of much of the Central European fossil record have also helped, especially in the case of the genomic analysis of aDNA from Vindija that demonstrates a Neandertal genetic contribution to living Eurasians.

Given the current evidence, we contend that Central European Neandertals were assimilated by early modern humans, contrary to either an overall in situ regional continuity or a complete replacement scenario. Although it is difficult to tell how much admixture took place in the region, the presence of more modern-like anatomy among late Neandertals and, more convincingly, the persistence of Neandertal features in early modern humans indicate that the degree of admixture exceeded that expected by interspecific hybridization. An improved fossil and archaeological record across the Neandertal-modern transition, further direct dating of fossils, more fossil genetic information, and the further application of additional analyses will help test this interpretation.

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Notes

1. In particular Cann et al., 1987.
2. See reviews in Relethford (2001a) and Cartmill and Smith (2009) for discussions of DNA studies on both extant and extinct humans.
3. Kleine Feldhofer Grotte, Mladeč, Krapina, Šal'a, Vindija, Kůlna, Peștera cu Oase, Muierii, and Cioclovina.
4. Although a tooth from Crvena Stijena (Montenegro) was originally published as Neandertal (Baković et al., 2009), its size and questions about its provenience may indicate otherwise (M. Roksandic, personal communication; R. Whallon, personal communication).
5. Part of the connecting highlands of eastern and western Central Europe.
6. Zeeland Ridges (Netherlands), Sarstedt, Hohlenstein-Stadel, Warendorf-Neuwarendorf, Hunas, and Ochtendung. A partial neonatal (or late-term fetal) skeleton from Sesselfelsgrötte preserves more of a single individual than any of the others, except for Feldhofer, but its young age (and fragmentary nature) makes interpretation difficult.
7. Interestingly, remains of the Barbary macaques (*Macacca sylvanus*) are found in earlier levels (Rosendahl et al., 2011).

8. The site of Crvena Stijena (Montenegro) contains a long Mousterian sequence topped by Aurignacian, Gravettian, and early Holocene deposits (Baković et al., 2009). Rare for a cave or rockshelter, a layer of volcanic ash from the Campanian Ignimbrite event is present in the deposits, marking the Middle/Upper Paleolithic boundary and dated to 39.3 ka (Morley and Woodward, 2011). During 2004, screening of slumped profile deposits (inferred to be from Basler's 1975 Middle Paleolithic levels), a single tooth was discovered (Baković et al., 2009). Baković and colleagues report that it is a Neandertal tooth but do not provide further clarification. Recent, unpublished analysis of the specimen by M. Roksanic indicates that the tooth is a left maxillary canine, and that, metrically, it falls below the Neandertal range and closer to Holocene modern humans (M. Roksandic, personal communication). Given the specimen's anatomy and that it was recovered from collapsed profile sediments, further interpretation of the Crvena Stijena tooth will have to await direct dating and/or genetic analysis (R. Whallon, personal communication).
9. Also known as Švédův stůl, after the name of the cave site.
10. The analysis of preserved faunal remains at Krapina indicates that the people living there exploited a wide variety of game, but it is also demonstrated that one of the animals well represented in the site is not the result of human activities (Miracle, 2007). The abundant cave bear remains at Krapina represent denning behavior after Neandertals abandoned the site. On the other hand, the extensive representation of rhinoceros remains do appear to be the result of human exploitation, probably mostly hunting, which further adds to the picture of Neandertals as top-level predators (Miracle, 2007).
11. A fragment of mandibular ramus (Vi 11.52) is labeled as coming from the older Level I, but this provenience is not certain (Ahern et al., 2004).
12. The G₁ assemblage also contains many Mousterian elements (Ahern et al., 2004).
13. Podbaba (Matiegka, 1924) and Silická Brezova (Vlček, 1957).
14. The eastern Central Europe cases involve skeletal remains that are intrusive into the levels they were initially reported from, and this intrusiveness was not recognized during excavation. This is true at both the Czech and Croatian sites (Table 5.1). At Velika Pečina, for example, there were skeletons from the Bronze Age discovered higher in the stratigraphic sequence, and it is likely that the Velika Pečina frontal belongs to this sample. It was originally thought to derive from level I at the site, associated with an undiagnostic Upper Paleolithic tradition and dated to ~34 ka (Smith, 1976a). The date for level I at the site is still valid for the early Upper Paleolithic in Central Europe, although it is an old, standard ¹⁴C date and thus may be an underestimate of the actual age. It is important to note that the Velika Pečina specimen did play an important role, despite the dismissal of its early Upper Paleolithic age (Smith et al., 1999). The description of the specimen (Smith, 1976a) made it clear that its browridge morphology was distinct from that of the Neandertals and helped demonstrate the fundamental difference between even earlier modern Europeans and late Neandertals, while at the same time suggesting the existence of some continuity between them (Smith, 1982). Thus, work on Velika Pečina contributed to the arguments, later developed into the Assimilation Model (Smith et al., 1989), concerning the pattern of later human evolution in Europe.
15. Attempts at directly dating this specimen have, thus far, been unsuccessful.
16. The slightly younger dates from Mladeč 25c and collagen from Mladeč 9 (brown collagen) are likely due to contamination (Wild et al., 2006).
17. Also known as mylohyoid bridging.
18. However, not all Gravettian humans lacked robust postcrania. The female skeleton Dame du Cavillon (France, formerly Homme de Menton) is far more robust than recent European males (Chevalier et al., in prep a,b; Voisin et al., in prep a,b).
19. Single nucleotide polymorphism.
20. Especially in the use of bipolar technology, see also Palma di Cesnola (1993).
21. For example, Kozłowski (2004) contends that the blade technology seen in the production of Upper Paleolithic tool types of the Bohunician, as well as the material from Temnata Cave in Bulgaria and Korolevo in Ukraine, arose directly from the Levallois tradition. The Szeletian and Streletskian types of leaf points, and likely Jerzmanowician, are modelled on the preceding Micoquian/Mousterian (also see Anikovich, 1992; Kozłowski, 1982).

22. For example, occipital morphology, morphology of the mastoid process, height of the cranial vault, morphology of the scapula axillary border, clavicle morphology, radius shaft, stature, and so forth. For a list, see Voisin, 2006.
23. Also, the “transitional” industries and the early Aurignacian generally lack any associated diagnostic fossils except for Vindija G₁, where potential level mixing complicates their interpretation.
24. Trinkaus (2007) reports the following Neandertal craniomandibular features present in the pre-Gravettian modern humans from Central Europe: (1) long, flattened frontal bones (Oase 2, Cioclovina 1, and Muierii 1); (2) occipital bunning (Muierii 1, Mladeč 3, 5, and 6) and hemibunning (Cioclovina 1, Mladeč 1, Oase 2); (3) lack of an external occipital protuberance, a medially limited nuchal torus, and an oval suprainiac fossa (Cioclovina 1 and Mladeč 6 except the latter has a broad nuchal torus); (4) a prominent juxtamastoid eminence (Oase 2, Mladeč 1, 2, and 5); (5) mandibular foramen lingual-bridging (Oase 1); (6) an asymmetrical mandibular notch (Muierii 1); (7) medially displaced mandibular notch crest (Muierii 1); (8) prominent lingual tubercle, marginal ridges, and a central lingual ridge on maxillary canines (Mladeč 9); and (9) a large ratio for front to back dental proportions reflecting large anterior teeth (Mladeč 54).
25. Furthermore, the degree of frequency difference between Neandertals and Upper Paleolithic modern humans for most of these traits is not statistically greater than what can be sampled from a comparison of Amerindian trait frequencies in Amerindians and postcontact Euroamericans (Ahern, 2006a).
26. As well as a slightly higher degree of Denisovan contribution to Melanesians (Reich et al., 2010).
27. Howell (1952) proposed that western Neandertals and modern humans were infertile contrary to more eastward populations. For Howell, this situation was due to complete isolation and genetic drift in the west part of the Neandertal distribution area caused by the extension of glaciers during cold periods that stopped gene flow between east and west populations.
28. The most striking examples of this are ring species like the salamander *Ensatina* or the greenish warbler *Phylloscopus* (Irwin et al., 2001a, 2001b, 2005).

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Chapter 6

The Makers of the Early Upper Paleolithic in Western Eurasia

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Introduction

The beginning of the Upper Paleolithic (UP) in Europe is marked by major biological and cultural changes. It coincided with the appearance of human populations, generally designated in the paleoanthropological literature as “anatomically modern humans” or “modern humans” (MH), in Europe. These humans display a morphological pattern clearly distinct from the preceding local Neandertal populations and are, in many of their known anatomical features, reminiscent of recent or extant humans. Important anatomical features include the presence of a shorter face, retracted under the neurocranium, and a braincase of globular form with well-developed parietal bossing. Their frontal bones are, in general, vertically oriented, with a supraorbital region displaying variably developed reliefs but disassociated into separate elements (*arcus superciliaris*, *trigonum supraorbitale*, etc.). Their temporal squamae are arched and elevated, while their occipitals are rounded and tilted postero-inferiorly. Their mandibles display a vertical or supero-posteriorly tilted symphyseal profile, a well-developed bony chin, and a mandibular body that declines in height posteriorly. They also lack the association of non-metrical dental features observed in Neandertals (Bailey, 2002). In addition, a series of postcranial characteristics—for example, the development of a protruding pilaster on the posterior side of the femur, straight radii, or a narrow pelvis—have been described as being unique to MH.

The notion that these anatomical novelties simply resulted from the *in situ* evolution of local Neandertals is no longer supported by most paleoanthropologists. They are rather seen as resulting from the appearance in Europe of new populations that were earlier documented in Africa and Southwest Asia. The lineage leading to UP and Holocene populations of Europe is phylogenetically distinct from that leading to the Neandertals, having evolved outside of Western Eurasia for most of the early Late and late Middle Pleistocene. A time of separation for the two lineages of at least 400 ka is deduced from paleontological and genetic evidence (Hublin, 2009). The late Middle Pleistocene or Late Pleistocene representatives of the MH lineage can be considered to be cladistically “modern.” However, although the definitions of anatomical and behavioral “modernity” are the topic of substantial disagreements,

it is important to emphasize that most of them were neither anatomically nor behaviorally fully “modern” if Holocene populations are used as a reference. Indeed a significant amount of biological evolution had taken place within the MH lineage since its divergence from the Neandertal lineage. Whether or not a speciation event or an accelerated evolutionary process occurred at any point along this lineage and gave rise to the genuine MH (or to “*Homo sapiens*” in the most restricted definition of this term) is still debated (see, e.g., Bräuer, 2008). However, even when a model of rapid emergence is accepted, differences in robusticity, as well as in morphology, can still be observed between “early modern humans” (EMH) who lived before 90ka BP in the Near East and Africa, those who are found in the early UP (EUP) of Europe, and more recent MH populations from the Holocene. Archaic traits, absent or very rare in extant populations but observed in older hominins, including Neandertals, were exhibited by these “early modern humans” before, and likely after, their initial appearance in Western Eurasia (e.g., Kupczik and Hublin, 2010).

For many scholars (e.g., Klein, 2009; Stringer, 2011), these major biological and behavioral changes in Western Eurasia are considered to have resulted from a process of peopling involving the arrival of allochthonous human groups. In this view the local archaic populations would have been primarily replaced through competition and/or mutual exclusion. However, an independent extinction of the Neandertals predating the arrival of MH (Finlayson et al., 2004) as well as an independent invention of the UP cultural suite by the European Neandertals (d’Errico, 2003) have also been proposed. From a genetic point of view, varying degrees of hybridization/assimilation between Neandertals and MH have been envisioned, ranging from trivial (Currat and Excoffier, 2004, 2011; Serre et al., 2004; Stringer and Andrews, 1988; Tattersall and Schwartz, 1999) to very significant (Brace, 1964; Duarte et al., 1999; Frayer, 1997; Smith, 1984; Trinkaus et al., 2003; Trinkaus and Zilhão, 2002; Wolpoff, 1999). One extreme version of these assimilation models considers the emergence of MH in Western Eurasia as resulting from genetic diffusion rather than from genuine replacement of the population. In this view a modern human phenotype would have spread across the world away from a distant African source mostly by local demic diffusion, hybridization, and natural selection (Eswaran, 2002; Eswaran et al., 2005). Crucial to all these debates is the demonstration or rejection of some level of morphological continuity between indigenous Neandertal populations and European UP MH groups.

The sequencing of the Neandertal mitochondrial and nuclear genome and its assessment in comparison to modern genetic variability has recently shed new light on these issues. To start with, these genetic studies have provided further arguments supporting the non-European origin of the UP populations of Europe. Furthermore, the integration of parts of the Neandertal genome into extant modern populations is detectable only at a low level (Green et al., 2010; Reich et al., 2010). As this genetic introgression did not leave demonstrably higher traces in the regions previously occupied by Neandertals than in other parts of Eurasia, including the Far East, it has been suggested that a limited amount of gene flow had occurred at the gate of Africa during, or even possibly before, the main phase of MH expansion onto Eurasia. Alternatively, if one assumes the much higher level of hybridization proposed by some (Duarte et al., 1999; Trinkaus, 2007), this would imply that Neandertal genetic material was erased from recent Western Eurasian MH populations by later extinctions and/or the replacement of populations or selection.

From a cultural point of view, the advent of the UP in Europe witnessed the development of an array of lithic assemblages, which sometimes overlapped temporally. In the window of time between 45 and 30 ka BP, three groups of lithic industries are found in Europe:

1. A variety of late Middle Paleolithic (MP) assemblages. In particular, this includes late denticulate Mousterian, Mousterian of Acheulean Tradition (MTA), and Micoquian.

2. Industries unfortunately called “transitional,” which suggests that they demonstrate a direct continuity between the local MP and UP. They generally display technological features inherited from the MP (local or not), for example, Levallois débitage. However, to various extents, they also forecast some of the cultural changes that characterize the later UP. These series of assemblages primarily include the Châtelperronian and Uluzzian in Western Europe, the Lincombian-Ranisian-Jerzmanowician (LRJ) in Northern Europe, and the Bohunian and Szeletian in Central Europe. To this group one can also add assemblages labeled “Initial UP,” as defined in the Near East (Kuhn, 2003) and some of the laminar assemblages with Mousterian reminiscence (Tsanova, 2008) observed in Eastern Europe (Tsanova and Bordes, 2003) and in the Near East (Kuhn et al., 2009).
3. A genuine “EUP,” mostly represented in Europe by the Aurignacian complex. Within this complex, a “proto-Aurignacian” (“Aurignacien archaïque” in Laplace terminology, see Laplace, 1966) has been identified in Southern Europe, in particular characterized by the production of large bladelets (Bartolomei et al., 1994; Bon, 2002). In some parts of Western Europe, the “proto-Aurignacian” is overlaid by an “Early Aurignacian.” However, north of the Alps, where the proto-Aurignacian is virtually unknown, the oldest Early Aurignacian assemblages are associated with ^{14}C dates ca. 39–38 ka ^{14}C BP (ca. 43–42.5 kcal BP)¹ as old as those of the “proto-Aurignacian” of Southern Europe (Douka et al., 2012; Haesaerts et al., 1996; Higham, 2010; Higham et al., 2011a; Nigst and Haesaerts, 2012). Therefore, rather than being two stages of the Aurignacian, the proto-Aurignacian and Early Aurignacian are increasingly being viewed as two pencontemporaneous lithic assemblages, the former developing in the Mediterranean areas and the latter along the Danube corridor, and overlapping in some limited geographical areas such as Southern and Central France. To highlight this situation, the term of “Fumanian” has been proposed to replace the term of “proto-Aurignacian” (Mellars, 2006). Unfortunately in the literature proto-Aurignacian assemblages from Southern Europe are still at times chronologically designated as “Early” Aurignacian.

Among the many questions surrounding the interpretation of this cultural division is the issue of its exact chronology and in particular the possible chronological overlap between late MP, “transitional” assemblages, and some EUP assemblages. Another important question is the biological nature of the makers of these different industries. To date all of the MP European sites with identifiable fossil human remains have only yielded Neandertal remains. Evolutionary models such as the pre-sapiens theory, directly rooting European modern humans in some peculiar local MP populations, retain only a historical value. The association of an “early anatomically modern human” child with a late Mousterian assemblage at Starosele (Ukraine) (Formosov, 1958), long believed to replicate the association of early MH and Mousterian assemblages of the Levant, has been demonstrated to result from late medieval Muslim burials being dug into a Paleolithic site (Marks et al., 1997). As no European site has ever yielded modern human remains in demonstrated association with any MP assemblage, one usually considers the recognition of genuine Mousterian or Micoquian assemblages in Western and Central Europe as a proxy for the past distribution of Neandertals in this area (but see Zwyns et al., 2012, contra Slimak et al., 2011).

Unfortunately, in most cases, transitional assemblages have not yet yielded diagnosable human remains, with the notable exception of the Châtelperronian, where Neandertal remains have been identified in at least two sites. However, the attribution of the Châtelperronian to the Neandertals is challenged by some authors (Bar-Yosef, 2006; Bar-Yosef and Bordes, 2010). The makers of the other transitional industries remain primarily unknown.

The Neandertal nature of the makers of the Uluzzian, LRJ, and Szeletian has sometimes been proposed based on very fragmentary evidence (Churchill and Smith, 2000; Gambassini et al., 2005; Palma di Cesnola, 1989; Palma di Cesnola and Messeri, 1967), or on the grounds of chronological arguments (Semal et al., 2009). However, this relation has been criticized based on a variety of reasons, and recent studies suggest that the Uluzzian was actually produced by modern humans (Benazzi et al., 2011). Aurignacian sites from Western Europe have yielded some human remains, though a series of discoveries in allegedly “EUP” contexts, which occurred during the pioneer times of Paleolithic archeology, have been proven to be questionable. Today one can relate human remains to a clear EUP archaeological context in only a handful of sites. In Central Europe more complete material has been assigned to the Aurignacian industries on the grounds of indirect or chronological arguments.

Revision of the Geological Age of EUP Human Remains

While reasonably complete Neandertal bone remains are easy to distinguish from recent modern human remains, this is not the case for UP MH remains. As a result, a number of modern human remains yielded by old and/or imprecise excavations, or found outside archaeological context, have been falsely assigned to the EUP. During the last two decades the improvement of ^{14}C dating, resulting in particular from the use of mass accelerators, which require only small samples, has made it possible to directly date UP fossil human remains. In the course of this process a number of more or less famous specimens previously thought to be EUP have been reassigned to more recent periods. Among them one should mention the fossils from Hahnöfersand 1 (Germany), Vogelherd/Stetten 1, 2, 3, and 4 (Germany), Velika Pećina (Croatia), and St. Prokop 1 (Czech Republic), which have been redated to the Holocene (Conard et al., 2004; Svoboda et al., 2004; Terberger et al., 2001). The remains from Zlatý kůň (Czech Republic) have been reassigned to the late UP, with a date of approximately 13 ka ^{14}C BP (15.9–15.1 ka cal BP) (Svoboda et al., 2002). One may also mention the skull from Kelsterbach (Germany), initially assigned to an early stage of the UP, based on a date of 32 ka ^{14}C BP (37.1–35.5 ka cal BP) (Protsch and Semmel, 1978). The specimen has since been lost, and one of the authors who produced these dates—and who was also involved in the first dating of the Hahnöfersand specimen—has been convicted of various scientific frauds.

The human remains from the Cro-Magnon shelter (France) deserve special attention. The series of skulls and postcranial remains discovered in 1868 have been generally considered as belonging to the late Aurignacian (Sonneville-Bordes, 1959), although during the 1960s they were already being attributed by some authors to the Gravettian (Vallois, 1971). The terms “Cro-Magnon Man” or “Cro-Magnon Race” then became synonymous with the “first modern humans in Europe.” To date, it has not been possible to obtain a direct date on these fossils. However, the dating of one of the periwinkle shells that was discovered in association with the human remains produced an age of $27,680 \pm 270$ ^{14}C BP (32.1–31.4 ka cal BP) (Henry-Gambier, 2002), contemporaneous with the Gravettian.

Regarding the transitional industries, one should also mention the human skeleton of Combe-Capelle (France). It has long been considered to be associated with the “Aurignacian type Châtelperronian” or “lower Périgordian,” that is, Châtelperronian in modern terminology, at the time of its discovery within the layers of the site (Peyrony, 1933). The doubts raised regarding this assignment (Asmus, 1964; Gambier, 1989) have recently been confirmed by direct dating of the specimen, demonstrating its Mesolithic age (Hoffmann et al., 2011).

Transitional Assemblages

Due to their “transitional” techno-typological pattern, it has often been assumed that most of these transitional assemblages were likely produced by late Neandertals. This notion has been fueled by the association of Neandertal remains with one of the assemblages. However, among the various so-called “transitional assemblages” described in Europe, very few human remains have been discovered. This is particularly true for Central and Eastern Europe, which is the area where modern humans most likely first settled in Europe, possibly carrying with them a material culture partly inherited from the late Middle Stone Age and/or late Middle Paleolithic of Africa and Southwest Asia. To date, out of this group of industries only the Châtelperronian has yielded significant human remains. One may add the Uluzzian and the Szeletian, which have provided much more fragmentary evidence.

The Châtelperronian has produced quite spectacular archaeological and paleontological material. It is known in Central and Southwestern France as well as in Northern Spain (Figure 6.5) and has been reported in more than one hundred localities. It is, however, important to underscore that only a handful of these sites have produced stratified sequences with more than one Châtelperronian layer and have yielded rich archaeological material with good bone preservation. The Châtelperronian is usually assigned to a window of time between 39 and 34 ka in ^{14}C (ca. 44–39 kcal BP) chronology (Figure 6.6). However most of the available ^{14}C dates are currently under revision, using increasingly more refined pretreatment techniques to resolve contamination problems at the limits of the range of the ^{14}C method.

The first site to produce human remains in Châtelperronian context is the site of Grotte du Renne at Arcy-sur-Cure, France. This cave was excavated between 1949 and 1963 by Leroi-Gourhan (1958, 1964). Its stratigraphy includes Mousterian layers (layer XIII–XI), three main Châtelperronian layers (X–VIII), a proto-Aurignacian layer (VII) (Bon and Bodu, 2002), and Gravettian layers (VI–IV). The Châtelperronian layers yielded a series of twenty-nine isolated teeth, some of them likely belonging to the same individuals, and various fragmentary skeletal remains, including an infant temporal bone. Most of this material comes from the lowermost Châtelperronian layer (layer X), but some also comes from layers IX and VIII. Already in 1958, Leroi-Gourhan (1958) suggested that the makers of the Châtelperronian in the Grotte du Renne could have been “Paleoanthropians” (i.e., Neandertals). This suggestion was based on the occurrence of primitive morphologies on the teeth as well as some level of taurodontism in the molars. A small number of the teeth described by Leroi-Gourhan were later proven to be non-hominin, but a confirmation of the Neandertal nature of this sample came from the study of the inner ear of the isolated immature temporal bone from layer X (Hublin et al., 1996). As with other Neandertals, the Arcy specimen displays, among other features, a semicircular posterior canal in a relatively low position relative to the lateral canal, when compared to modern humans. This interpretation has been confirmed by further studies of the Neandertal labyrinth (Spoor et al., 2003), which have shown that the Arcy specimen was not at the fringe of the morphological variation of the group but rather displayed typical Neandertal morphology.

The large dental series from Arcy-sur-Cure has recently been analyzed in several papers, mostly addressing non-metrical features (Bailey et al., 2009; Bailey and Hublin, 2006; Hublin et al., 2006) (Figure 6.1). These features are observed with different frequencies in Neandertals and MH. One extreme case is the frequency of the mid-trigonid crest on the lower first molars, which reaches 98.6% in Neandertals compared to 0% in UP modern humans (Bailey et al., 2011). Relying on different frequencies for non-metrical features in Neandertal and MH comparative samples, it is possible to compute a Bayesian posterior probability for each indeterminate tooth or group of teeth of the same individual as being

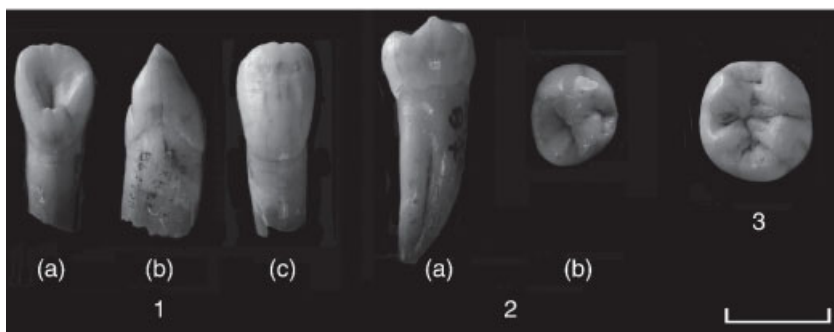


Figure 6.1. Example of dental remains from the Châtelperronian layers of the Grotte du Renne (Arcy sur Cure, France), displaying Neandertal features. (1) I² (Tooth #23): (a) lingual view, (b) buccal view; (2) left P₄ (Tooth #4): (a) lingual view, (b) occlusal view; (3) right M₁ (Tooth #35): occlusal view (for inventory see Bailey and Hublin, 2006). Photo Shara Bailey.

assigned to one group or to the other. At the Grotte du Renne all but one Châtelperronian individual were assigned to the reference Neandertal group with posterior probabilities ranging from 59% to 99.9%. Just one partial crown was assigned to UP modern humans, but only with a low posterior probability of 54% (Bailey et al., 2009). From a metrical point of view, the Grotte du Renne teeth also display large anterior dimensions relative to the posterior ones reminiscent of the Neandertal conditions. Bucco-lingual dimensions of the lower lateral incisors and canines fall outside of the range of a comparative Upper Paleolithic sample (Hublin and Bailey, 2006). The Grotte du Renne Châtelperronian series therefore yields an overwhelmingly Neandertal signal.

The second main site that has yielded Neandertal remains in a Châtelperronian context is the site of Saint-Césaire (France). In 1979, during the excavation of the rock shelter of La Roche-à-Pierrot by François Lévêque, a fragmentary skeleton was discovered, including the face and the right half of the braincase, a large portion of the mandible, isolated teeth, and many fragments from the postcranial skeleton. The specimen Saint-Césaire 1 was unearthed from the layer EJOP superior. The fact that the human remains were concentrated inside a rather small area of about 70 cm in diameter led (Vandermeersch, 1993) to hypothesize that it could have been a secondary burial. However, the grouping of the bones and their damage could alternatively have resulted from the action of solifluxion and water circulation on a primary burial. To date, the specimen has only partially been published. Lévêque and Vandermeersch (1980) identified the specimen as Neandertal and partial descriptions by other authors (Stringer et al., 1984; Trinkaus et al., 1998), have confirmed this assignment, emphasizing the degree of midfacial prognathism, the dental-arc shape, the supraorbital morphology, the vault shape, the temporal morphology, the hyper-arctic body proportions, the dorsal scapular groove, and the curved radius with a medially placed radial tuberosity. Some aspects of the anatomy of the specimen have also been claimed to differ from the most usual Neandertal morphology (Wolpoff, 1999). This includes a lateral reduction of the supraorbital torus, an unusually narrow nasal aperture, rather squared orbits, and some reduction of the anterior dentition. However these features have occasionally been found in older representatives of Neandertals and considering the scarcity of Neandertal remains associated with the transitional assemblages, it is difficult to assess whether this pattern simply results from individual variation or from a consistent evolutionary trend. Morphologically, the teeth of the Saint-Césaire specimen display a clear Neandertal morphological pattern (Bailey et al., 2009), with a posterior probability computed to 98% for Saint-Césaire 1 being a Neandertal. At least one additional individual has been found at

Saint-Césaire (Saint-Césaire 2), represented by an upper canine and an upper M2. A lower probability of 66% of being a Neandertal was computed for this individual, most likely because the three accessible traits on this composed individual display a minimal difference in frequency between Neandertals and UP moderns.

The association of Neandertal remains with Châtelperronian assemblages in Arcy-sur-Cure and Saint-Césaire has been much discussed. At the Grotte du Renne, the debate also surrounds the origin of body ornaments and manufactured bone objects found in layers X to VIII (d'Errico et al., 1998; Hublin et al., 1996, 2012a; White, 2001). The most parsimonious interpretation is to acknowledge the association of Châtelperronian stone artifacts, body ornaments, and Neandertal human remains. For those who accepted this association, Neandertals were seen as being the makers of these material productions. The new behavior of piercing or grooving teeth or other objects to produce beads during the time of the very last Neandertals may have resulted from either the distant influence of contemporaneous modern humans already present in Europe (Harrold, 1989; Hublin et al., 1996, 2012a; Mellars, 1999) or from an "independent" innovation process within the last Neandertal populations (d'Errico, 2003). For those who question this association, the integrity of the layers in Arcy have been challenged (Higham et al., 2010), as well as the association of Neandertal remains with the Châtelperronian industry (Bar-Yosef and Bordes, 2010). Bar-Yosef and Bordes (2010) reject the Neandertal nature of the makers of the Châtelperronian and identify this assemblage as being a genuine Upper Paleolithic industry made by modern humans predating the Aurignacian in Western Europe. This view is primarily based on typotechnological and stratigraphic arguments. According to these authors, the Châtelperronian would have no relation with the local late Mousterian (MTA), as it has generally been assumed (Pelegrin and Soressi, 2007). Instead, the Châtelperronian would forecast the later proto-Aurignacian. It remains, however, puzzling to note that the MTA and the Châtelperronian display almost exactly the same limited geographical distribution at the western end of Europe, while the proto-Aurignacian style assemblages are dispersed on an area ranging from Bulgaria to Spain and have tentatively been linked to the Early Ahmarian (Bar-Yosef, 2003; Mellars, 2006; Teyssandier, 2007; Teyssandier et al., 2010; Tsanova et al., 2012; Zilhão, 2006). At Grotte du Renne it has also been argued that Neandertal remains could have been reworked from the underlying Mousterian layers into the Châtelperronian layers by modern human settlers. This seems inconsistent with the fact that these underlying Mousterian layers contained very few human remains in comparison to what has been found in the overlaying Châtelperronian layer. In addition, these Neandertal remains were not only found in the lowermost Châtelperronian layer in contact with the last Mousterian layer. The uppermost Châtelperronian layer (layer VIII) also yielded at least two teeth, most likely Neandertal, in an undisturbed area of the site. The selective migration of Neandertal teeth through the stratigraphy upward seems as unlikely as the selective migration of Aurignacian body ornaments downward through three Châtelperronian layers that otherwise do not display many signs of admixture when the lithic evidence is considered (Caron et al., 2011). The possibility in Saint-Césaire of a secondary burial "planted" by contemporaneous Neandertals into the occupation site of neighboring modern humans as suggested by Bar-Yosef and Bordes (2010) seems equally non-parsimonious. A recent reexamination of the Châtelperronian lithic assemblage at the site of Quinçay by Roussel (2011) has shown that the Châtelperronian makers produced large bladelets, looking like those found in the proto-Aurignacian but produced through a different technological pathway. This observation is more in agreement with the acculturation at distance model rather than with that of a vertical filiation between the Châtelperronian and proto-Aurignacian.

Based on chronological reasoning, it has also been proposed that the LRJ found in Northwestern Europe would have been produced by late Neandertals from the area

(Semal et al., 2009). The argument relies on the direct dating of the Spy (Belgium) Neandertals, which produced a rather late age ca. 36 ka ^{14}C BP (ca. 41 ka cal BP). These human remains were unearthed in 1885–1886 and have traditionally been associated with the upper Mousterian layers of the site (e.g., Zeuner, 1940). However, LRJ and Aurignacian assemblages are also represented in the stratigraphy of the Spy site and considering the poorly recorded circumstances of the discovery it is difficult to support a well-demonstrated Mousterian assignment of the Neandertal skeletons found in the site. Semal and Coll (2009) have argued that in this part of Europe there is no convincing evidence of a Mousterian as young as the direct dates obtained on the Spy Neandertal remains. The age of these remains would rather match the time period when the LRJ developed. This indirect association of the LRJ with Neandertals should of course be substantiated with more discoveries for a direct association to be proven.

To date only two deciduous teeth (a left dm1, Cavallo B, and a right dm2, Cavallo C) from the Grotta del Cavallo (Italy) have been described in Uluzzian context. Above the Mousterian layers, the stratigraphy of the cave displays several Uluzzian layers (E-DIb), which are covered by a stalagmitic crust and by tephra layers (layer C), traditionally assigned to the Campanian Ignimbrite eruption. Above the tephra come Epigravettian horizons. Cavallo B was recovered in layer EIII (archaic Uluzzian) and Cavallo C in layer EII-I (evolved Uluzzian). The teeth were initially classified as belonging to MH (Cavallo B) and Neandertal (Cavallo C) and, as a result, it was hypothesized that the latter hominin survived for some time after the arrival of the former (Palma di Cesnola and Messeri, 1967). On metrical and morphological grounds, in particular due to some level of taurodontism, both teeth were later attributed to Neandertals (Churchill and Smith, 2000; Palma di Cesnola and Messeri, 1967). These classifications were probably influenced in part by the notion that the Uluzzian, like the Châtelperronian, could be the result of the evolution of the local Mousterian. A recent reassessment of this material (Benazzi et al., 2011), based on morphometric analyses of the crown outlines and of the enamel thickness, has resulted in the attribution of both specimens to MH. New ^{14}C dates obtained on shells from the site are consistent with an assignment of the tephra to the Campanian Ignimbrite eruption, dated at $39,300 \pm 55$ BP by $^{40}\text{Ar}/^{39}\text{Ar}$ (De Vivo et al., 2001; Pyle et al., 2006). A shell from the level that yielded the most recent of the two teeth provided an age of about 40 ka ^{14}C BP (or 43 ka cal BP), which should represent a *terminus ante quem* for Cavallo-B and for the arrival of modern humans in the cave (Benazzi et al., 2011). At the Grotta del Cavallo, possible admixture of Uluzzian and Aurignacian assemblages in the uppermost Uluzzian levels of layer D has been claimed by Gioia (1990). Radiocarbon dating on a shell fragment of a bivalve from layer DII has produced an older determination than any other obtained for the Grotta del Cavallo sequence (Benazzi et al., 2011), potentially corroborating the hypothesis that mixing had occurred in this part of the deposit. However, even if demonstrated, this mixing is unlikely to have affected the lower Uluzzian archeological layers, where Cavallo B was discovered.

Farther east, at the Bacho Kiro cave site (Bulgaria), a fragment of the left side of a mandibular corpus, bearing a first deciduous molar, was yielded by layer 11, which underlies the Aurignacian and contains a “Bachokirian” assemblage (Gleń and Kaczanowski, 1982). Charcoal from the top of layer 11 was dated by conventional ^{14}C to >43 ka ^{14}C BP (Mook, 1982). However, layer 11 also provided more recent AMS dates of ca. 39–38 ka ^{14}C BP (43.2–42.4 ka cal BP) (Hedges et al., 1994). Layer admixture is unlikely, as the abundant lithic assemblage of this layer is technologically homogeneous and clearly distinct from that of the overlying Aurignacian (Tsanova and Bordes, 2003). One can rather suspect issues with the pretreatment of the ^{14}C samples, which is crucial for this time period and was much improved in the last decade (Higham, 2010). Like the Bohunician from the Czech Republic (Svoboda and Bar-Yosef, 2003), the Bachokirian is characterized by the use of Levallois

technology to produce elongated blanks. At Bacho Kiro these blades have been retouched in particular to produce endscrapers. Although some have related the Bachokirian to the local Mousterian (Tsanova and Bordes, 2003), it should be emphasized that this expression of the Levallois technology is quite reminiscent of the assemblages from the Near East at Bocher Tachtit (Israel) or Umm el Tlel (Syria) (Marks, 1983), in which the local initial UP could be rooted. It is therefore of the utmost importance to identify the makers of assemblages such as the Bohunician or the Bachokirian in Central Europe. In their original description, Gleń and Kaczanowski (1982) suggested that the specimen could be closer to the Neandertal morphology, mostly because of its large bucco-lingual diameter. Unfortunately, the original material from Bacho Kiro layer 11 has been lost, and it is therefore impossible to assess truly discriminant features on the dm1 such as enamel thickness or cervical outline. One cannot reject the possibility that this specimen enters the variation of MH.

The last “transitional assemblage” with which some humans could be associated is the Szeletian of Central Europe, but this assignment is quite dubious. From the Upper (“Felső”) Remete Cave, near Máriaremete (Hungary), three worn teeth (right I_1 , I_2 , and C_1), probably from a single individual, were published as Neandertals based on the measurements of the canine (Kretzoi, in Gábori-Csánk, 1983). The very poor lithic assemblage associated with these remains was initially assigned to the “Trans-Danubian Szeletian” or Jankovichian (Gábori-Csánk, 1983). The archeological record of the Jankovichian is quite problematic (Svoboda and Siman, 1989), and in the case of the Remete cave, it seems most likely that the assemblage represents a late Micoquian with some foliate elements (Allsworth-Jones, 1990; Gábori-Csánk, 1983).

Proto-Aurignacian

Human remains found in proto-Aurignacian contexts are extremely scarce. In the site of Le Piage (France), skeletal fragments of a fetus (or newborn) have been discovered in a proto-Aurignacian layer but have remained unidentifiable (Beckouche and Poplin, 1981). Since then, dental material has been yielded by the site but is still unpublished. A left deciduous incisor from layer III at Riparo Bombrini (Italy) is also associated with the proto-Aurignacian complex (Vicino, 1986). The crown is of rather small dimension and its morphology is said to be modern (Formicola, 1989). No dates are available for the context in which this tooth was recovered, but at the nearby site of Riparo Mochi, another rockshelter at Balzi Rossi, the proto-Aurignacian has recently been dated to start at ~ 37 ka ^{14}C BP or ~ 42 kcal BP and to have lasted almost five thousand years (Douka et al., 2012). The tooth from Riparo Bombrini, therefore, probably dates to this interval of time, but a more refined chronological attribution could only be obtained through dating the stratigraphic sequence of the site where it was recovered. This very modest fossil does not display obvious Neandertal affinities.

In Isturitz (France), some fragmentary human remains were originally assigned to the broad “Aurignacian” division of cave (“couche A” by Passemard 1944 or “couche V” by Saint-Périer and Saint-Périer, 1952). The “Aurignacian” of Isturitz displays clear proto-Aurignacian assemblages (layer C4d1) and overlying deposits displaying proto-Aurignacian and Early Aurignacian traits in layer C4c4 (Szmids et al., 2010). Layer C4c4 provided a series of radiocarbon dates with a weighted mean of $37,180 \pm 420$ ^{14}C BP (42.3–41.6 kcal BP). Unfortunately, the human cranial fragments allegedly yielded by the different layers of the site can be refitted, and the ubiquitous presence of cutmarks on all these remains originally assigned to layers ranging from the Aurignacian to the Azilian suggest that in fact all the remains may be derived from one layer only, likely the Magdalenian level of the site, by far the richest in human remains (Gambier, 1990).

In Spain, the fossil material discovered by H. Obermaier in the El Castillo cave before the First World War is assigned to layer 18, as defined by the new excavation by V. Cabrera Valdés after 1980. This layer has been considered to represent an “Early Aurignacian” or a “Transitional Aurignacian” for Cabrera Valdés and Bernaldo de Quiros (1996), who assume its emergence from the local MP. Layers 18b and 18c of new excavations yielded some lithics that fit better with the proto-Aurignacian than Early Aurignacian, but also lithics that would fit well into underlying Mousterian layers. Furthermore, the radiometric dates obtained in layer 18 range from 42.2 to 37.1 ka ^{14}C BP (46.2–41.9 kcal BP) (Cabrera Valdés and Bernaldo de Quiros, 1996). Therefore, the hypothesis of an admixture of industries could be considered as an alternative explanation for the mixed techno-typological pattern of the layer. Unfortunately, the human remains were lost before being published. Three individuals may have been represented by cranial fragments, a second right lower molar and a fragmentary child mandible bearing a dm1 and dm2 on the right side as well as an unerupted right M1. An unpublished description by Vallois has been made available and was commented on by Garralda et al. (1992) but does not allow for a clear taxonomical assignment of these specimens.

Early Aurignacian

A series of specimens has been assigned to the “Early Aurignacian” in Central and Western Europe on the grounds of archaeological association. Additional discoveries out of any archaeological context, but nevertheless contemporaneous with an early phase of the Aurignacian in their geographical domain, should be added to this list.

In Bacho Kiro, Bulgaria, several fragmentary specimens have been found in the “Aurignacoid” layers 6–7, which overlie the Bachokirian layers and are poor in archaeological remains. Among them one should mention a fragment of right parietal, a lower right permanent central incisor, a lower right lateral incisor, a right premolar, an upper right permanent canine, a deciduous lower central incisor, and a fragment of an immature right mandible bearing the second deciduous molar and the first permanent molar (specimen #599) (Gleń and Kaczanowski, 1982). Layer 7 has produced an AMS date from charcoal at $32,200 \pm 780$ ^{14}C BP (37.9–35.5 kcal BP) (Hedges et al., 1994). Churchill and Smith (2000) generally concluded that these Bacho Kiro specimens are ambiguous but closer to modern humans. The reexamination of specimen #599 by Bailey et al. (2009) assigned the specimen to the UP MH group with a moderate posterior possibility (66%) based on six non-metrical traits.

A human lower right M2 (although a lower M1 cannot be discounted) was discovered in UP context predating 34 ka ^{14}C BP (~39 kcal BP) in Slovakia at Dzeravá Skala (Kaminská et al., 2004). The specimen was initially described by Hillebrand (1914) as Neandertal; however, this tooth, which displays four cusps and lacks a midtrigonid crest, is actually quite modern in its morphology. The Bayesian assessment of its non-metrical features assigns it to the UP MH with a posterior probability of 100% (Bailey et al., 2009). The positive association of this material with the Early Aurignacian is unclear, as the sedimentation processes in the site were rather chaotic and the layers are affected by cryoturbation and mechanical disturbances (Kaminská et al., 2005). As the layer also contains foliate elements, the tooth was also sometimes assigned to Szeletian (Churchill and Smith, 2000; Hillebrand, 1914).

Further west, at Fossellone, one of the caves of the Monte Circeo (Italy), a maxillary fragment (Fossellone 1), could be associated with a rather early Aurignacian (Mallegni and Segre-Naldini, 1992). The morphology of Fossellone 1 indicates a deep canine fossa and the associated M2 was described as falling into the modern UP variability (Mallegni and Segre-Naldini, 1992). A scapula fragment (Fossellone 2) of modern morphology is also reported from the site, but its chronostratigraphic context is uncertain. At Fontana Nuova di Ragusa,

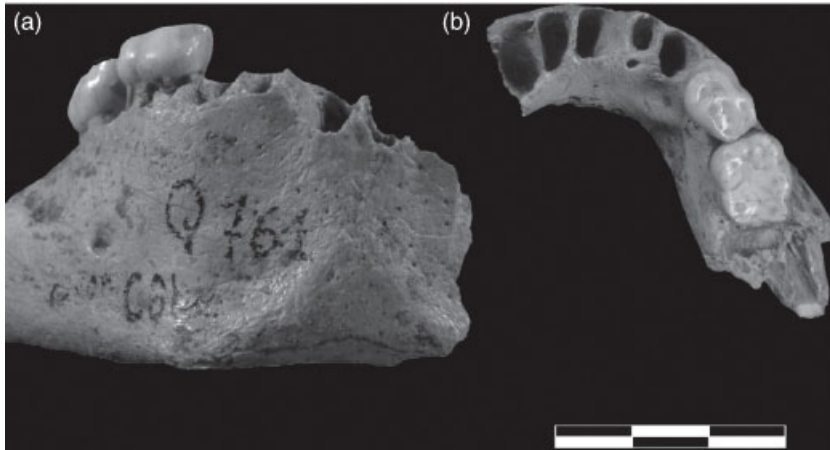


Figure 6.2. La Quina-Aval 4 mandible: (a) anterior view, (b) occlusal view. Photo Christine Verna.

in the south of Sicily, a few human remains (a parietal, a frontal fragment, a talus, a left maxillary P3 and a right maxillary M2), without any clear taxonomical assignment (Chilardi et al., 1996), have been considered to be associated with an Early Aurignacian lithic assemblage. However, the extraordinary conditions of their discovery (the bones were recovered by L. Bernabò Brea in the spoil heap of the original unsystematic excavations) and the suggestion that the lithic assemblage is typologically assignable to the Late Epigravettian industry (Martini et al., 2007) throw doubt on the attribution of Fontana Nuova to the Aurignacian.

Human remains yielded by some French sites are assigned to Early Aurignacian assemblages. In La Ferrassie, one upper first left incisor has been described (Gambier et al., 1990). In Fontéchevade, one fragmentary child mandible, an upper first molar and a fragmentary adult parietal may also come from a rather ancient part of the Aurignacian layers (Garralda, 2006; Chase and Teihol, 2009). One of the most securely dated sets of specimens comes from the site of Brassempouy (Henry-Gambier et al., 2004). This site has yielded a dental series, a fragment of mandible, a cranial fragment, and two distal hand phalanges in a well-recorded stratigraphical context. The layers that yielded this material have produced dates in a window between 35 and 30 ka ^{14}C BP (ca. 40.5–35 ka cal BP) (Henry-Gambier et al., 2004). As is generally the case, the metrical analysis of the isolated teeth did not allow for a clear taxonomical assignment (Henry-Gambier et al., 2004). However, the assessment of non-metrical traits has been revealed to be a much more powerful tool in distinguishing the Neandertal versus MH morphologies in these series. At Brassempouy the modern signal is quite clear. Four individuals display a 90% and one a 63% posterior probability of being modern (Bailey et al., 2009; Bailey and Hublin, 2005).

Even more complete remains come from the site of La Quina-Aval (France) where Early Aurignacian layers dated at 32.6 ka ^{14}C BP (41.7–40.9 ka cal BP) (Dujardin, 2005) have also yielded human remains. Among the preserved material, two immature mandibles and a lower premolar have been identified. The mandible Quina-Aval 4 displays a dental arc that is anteriorly narrow and possesses a clear bony chin (Figure 6.2). The associated dental material does not display any Neandertal features and there is little doubt about the modern nature of this collection, which to date likely represents the best evidence in Western Europe of the modern nature of the Early Aurignacian assemblage makers (Verna et al., 2009).

For phases of the Aurignacian predating 34.0 ka cal BP in Eastern Europe one should also mention human remains that were discovered at Kostenki 14 (Markina Gora, Russia), where

the easternmost Aurignacian (in a European sense) is observed (Sinitsyn, 2003; Zwyns and Flas, 2010). A complete skeleton was discovered in a pit dug through a layer of volcanic ash, which has tentatively been related to the Campanian Ignimbrite (CI) super-eruption (Pyle et al., 2006). It is overlaid by a Gorodzovian layer dated between 31.8 and 28.4 ka ^{14}C BP (36.7–32.7 ka cal BP) (Krause et al., 2010) and seems to be associated with an Aurignacian assemblage of the ash layer. Direct dating of the remains gave inconsistent results due to contamination by consolidant (Sinitsyn, 2004). Up until now, only preliminary descriptions of the remains have been published (Debets, 1955; Gerasimova, 1987). The specimen is a young adult male of rather short stature (ca. 165 cm according to Gerasimova, 1987). Debets (1955) emphasized the lack of Neandertal-like features and similarities in the facial proportions with the Grimaldi material. Based on the comparison of the Kostenki 14 individual's complete mitochondrial sequence with extant references, a molecular best age estimate of 32.7 ka has been proposed (Krause et al., 2010). This age is compatible with a ^{14}C date on charcoal at $32,420 \pm 440$ ^{14}C BP (37.5–36.4 ka cal BP) in the Aurignacian layer and with stratigraphic correlations assigning the Aurignacian assemblage to a window of time between 33 and 30 ka (Haesaerts et al., 2004). If confirmed, the assignment of the Kostenki individual to the Aurignacian would make it the only burial and the only articulated skeleton ever found in this archeological context. One should also mention that at Kostenki 1 (layer III) an undescribed human tibia and fibula were found in an Aurignacian context and directly dated at $32,600 \pm 1,100$ ^{14}C BP (38.8–35.7 ka cal BP) (Richards et al., 2001).

In a similar window of time, a human distal thumb phalanx has been directly dated at $31,000 \pm 550$ at the cave of Oblazowa (Poland) (Hedges et al., 1996). A much larger series of human remains, undisputedly modern although fragmentary, come from the site of Buran-Kaya III (Ukraine). One of these fragments is directly dated at $31,900 \pm 240$ ^{14}C BP (36.7–35.7 ka cal BP) (Prat et al., 2011). In both cases the archeological context is said to be related to the Gravettian. However the radiometric ages obtained in both sites make this questionable. This is especially true for Buran Kaya III where ^{14}C dates from $34,050 \pm 260$ ^{14}C BP (39.2–38.6 ka cal BP) to $34,910 \pm 950$ ^{14}C BP (40.9–38.9 ka cal BP) have been obtained in the lower part of the allegedly Gravettian layers. Alternatively this assemblage could be related to the EUP assemblages such as those discovered in the Caucasus (Bar-Yosef et al., 2006; Golovanova et al., 2006).

At Peștera cu Oase (Romania) human remains were discovered in the depths of a karst outside of any archaeological context (Rougier et al., 2007; Trinkaus et al., 2003). The two main specimens are a mandible (Oase 1) (Figure 6.3) and the skull of a separate adolescent individual (Oase 2). For the skull, the direct dating provided only a minimal age of > 29 ka ^{14}C BP, but the direct dating of the mandible provided an age of $34,290 \pm 970$ – 870 ka ^{14}C BP (40.7–38.4 ka cal BP) and an age of $> 35,200$ ka ^{14}C BP (Trinkaus et al., 2003). These dates roughly correspond to the window of time of the Early Aurignacian and “proto-Aurignacian” in Central Europe. It has also been proposed that they might be the skeletal remains of the makers of one of the local “transitional” industries, such as the Bohunician (Stringer, 2011). However, the bulk of the available radiometric data, and more importantly the geological context in which such assemblages are found in open-air sites of Central Europe, clearly suggest a more ancient geological age, beyond 39 ka ^{14}C BP (43 ka cal BP) for these assemblages (Svoboda and Bar-Yosef, 2003; Richter et al., 2009). The human remains from Peștera cu Oase are clearly modern, and the mandible Oase 1 is to date the oldest directly dated and well-identified MH discovered in Europe (Trinkaus et al., 2003). Its general proportions are modern, and it displays a prominent *tuber symphyseos*, a symmetrical mandibular incisure, medially placed condyles, small superior medial pterygoid tubercles, a mesially located mental foramen, and a narrow corpus. The skull has also been described as displaying a full suite of modern features (Rougier et al., 2007). It includes a high neurocranium



Figure 6.3. The mandible from Peștera cu Oase (Romania). Photo: Eric Trinkaus/Romanian Academy.

with prominent parietal bosses and a marked sagittal parietal curvature, the absence of a supraorbital torus, vertical auditory porous, laterally bulbous mastoid processes, and the absence of both a nuchal torus and suprainiac fossa. On the face, the orbits are subrectangular, there is a prominent canine fossa, angled and anteriorly oriented zygomatic bones, a narrow nasal aperture, a level nasal floor, and a superiorly positioned temporal zygomatic root. A couple of features of the Peștera cu Oase specimens are at a variance with the conditions observed in most recent MH. In particular, the posterior dentition is exceptionally large, and molar size increases from M1 to M3. On the mandible, one of the two mandibular foramina displays a horizontal oval pattern more frequent in Neandertals than in MH (Trinkaus et al., 2003). On the skull, the low convexity of the frontal bone and the strong development of the juxtamastoid eminence have also been highlighted as being unusual (Rougier et al., 2007). According to Rougier et al. (2007), these features may have resulted from direct gene flow between local Neandertal populations and early MH moving into Eastern Europe. Alternatively these authors admit that these features could also have been inherited from early modern African ancestors.

Later Aurignacian

For the period around 35 cal BP and later, more abundant material has been discovered. The most spectacular series comes from Mladeč (Czech Republic) (Figure 6.4). The main cave in this location was excavated at the end of the nineteenth century and the beginning of the twentieth century and has yielded no fewer than a hundred identifiable human remains. Unfortunately, more than half of them were destroyed in the last days of the Second World War. This collection consists of two skulls and two skullcaps, associated mandibles, postcranial bones, and immature remains. The site conditions suggest a rapid deposit of a block of sediment through a chimney connecting the karst to the surface (Svoboda, 2000). The archaeological context is limited but includes a series of twenty-two bone points as well as some fragments of “poinçons” and a series of perforated teeth. The archeological remains



Figure 6.4. Main specimens from the Mladeč series (Czech Republic). Photo: M. Teschler-Nicola.

found in the Mladeč sites characterize a middle phase of the Aurignacian in Central Europe. Moreover, the Aurignacian assignment of the human remains has been confirmed by direct dating of the skulls (Wild et al., 2005). Four samples have yielded radiometric ages averaging ca. 31 ka ^{14}C BP (ca. 35.5 ka cal BP). The cranial and mandibular morphology of the Mladeč humans is clearly modern (Bräuer et al., 2006; Wolpoff et al., 2006). However, some anatomical details have been highlighted, by supporters of the local continuity of the human peopling in Europe, as being possibly inherited from local Neandertals (Fruyer, 1986; Fruyer et al., 2006; Wolpoff et al., 2006). This includes the shape of the neurocranium with a marked bun (but see Gunz and Harvati, 2007), and the possible persistence of a faint suprainiac fossa on Mladeč 6. The analysis of the non-metrical dental features provided a mixed signal (Bailey et al., 2009). The partial maxillary dentition of Mladeč 1 is classified as MH with a posterior probability of 99% based on six traits. However, the classification of Mladeč 2 as MH is obtained with a probability of only 53%, but the most diagnostic traits cannot be assessed. A composite individual made with two teeth from Mladeč 9 and the M3 of Mladeč 10 was contrastingly assigned to the Neandertal group with a posterior probability of 80%, mostly resulting from the features of the canine of Mladeč 10.

Other modern specimens have been discovered in the Southern Carpathians (Romania) in the cave of Muierii, where Aurignacian layers have been identified. (Alexandrescu et al., 2010). A human skull from this site has been directly dated to $30,150 \pm 800$ ^{14}C BP (36.1–33.7 ka cal BP). The site has also produced a mandible and postcranial fragments. Another very complete specimen comes from the cave of Cioclovina, where Aurignacian assemblages have also been discovered. The Cioclovina skull is dated to $29 \text{ ka} \pm 700$ ^{14}C BP (34.4–33.1 ka cal BP). In both sites the human skulls are anatomically modern (Harvati et al., 2007; Soficaru et al., 2006, 2007). Some anatomical details, including the occurrence of a suprainiac fossa, have been proposed by Soficaru et al. (2006, 2007) as being archaic or possibly Neandertal retentions. However, a geometric morphometric analysis conducted by Harvati et al. (2007) concluded that the anatomy of the skull is fully modern and, as in Mladeč, the suprainiac fossa does not display a Neandertal pattern but rather reflects recent

MH populations. More fragmentary human remains have also been assigned to the Aurignacian complex in the caves of La Adam, Bordu Mare, Peștera Mică and Malu Roșu (Alexandrescu et al., 2010).

In addition, an isolated lower M1 should be mentioned from the site of Istállóskő (Hungary), which has been assigned to the Lower Aurignacian or even the Bachokirian and related to a date of 39.7 ka ^{14}C BP (44.2–43.3 ka cal BP) (Allsworth-Jones, 1990). However, according to the description of the discovery by Malan (1955), the tooth comes from the upper Aurignacian layer and would therefore be dated somewhere between 31 and 28 ka ^{14}C BP (36.1–32.2 ka cal BP) (Adams and Ringer, 2004). Its morphology is fully modern and lacks any Neandertal non-metrical trait (Bailey et al., 2009). Another specimen from the site of Görömböly-Tapolca, in the Bükk mountains (Hungary) should be mentioned. It is a modern occipital bone (Thoma and Vértes, 1971) that has been directly dated at 30,300 \pm 300 ^{14}C BP (35.0–34.6 ka cal BP) (Davies and Hedges, 2008–2009).

In Western Europe some human fragments have been assigned to middle phases of the Aurignacian. In Germany one should mention the sites of Hohlenstein-Stadel, Sirgenstein, Kleine Ofnet, Schafstall, and Geißenklösterle (Czarnetzki, 1983; Orschiedt, 2000; Street et al., 2006). In France one artificially perforated lower first or second left molar comes from La Combe (White et al., 2003), but the most complete remains have been discovered in the caves of Les Rois and La Crouzade. In the first site several remains have been yielded by layers dated between 30 and 28 ka ^{14}C BP (34.6–32.4 ka cal BP) (Ramirez Rozzi et al., 2009). The series is composed of thirty-seven isolated teeth, a rather complete immature mandible (Mandible A), and a smaller mandibular fragment (Mandible B). Mandible A displays a clear modern morphology (Gambier, 1989; Ramirez Rozzi et al., 2009; Vallois, 1958; Verna et al., 2008), in particular the occurrence of a bony chin. Mandible B shows some cutmarks and was found higher in stratigraphy. Although the specimen is quite fragmentary, Ramirez Rozzi et al. (2009) identified some features in the dental microstructure pattern that would exceed the limits of modern variability, in particular in the spacing of the perikymata on the dental crowns. Although the evidence is limited, these authors entertained the possibility that this specimen could actually be that of a Neandertal which had been consumed, or “more likely” (*sic*) would represent an object symbolically used by modern humans. Alternatively, the makers of the Les Rois Aurignacian might represent a mixed MH/Neandertal population or a population of MH with a variation for this feature different from that observed in extant MH. In La Crouzade, the best preserved specimens are represented by a frontal bone (La Crouzade V) and a maxilla (La Crouzade VI). The maxilla has been directly dated at 30,640 \pm 640 ^{14}C BP (36.2–34.6 ka cal BP) (Henry-Gambier and Sacchi, 2008). The dentition fits within modern variability and the frontal bone is quite modern in its general proportions and curvature and in the morphological details of its supraorbital area, which display dissociated elements (Henry-Gambier and Sacchi, 2008).

Discussion and Conclusion

In the last decade, the direct dating of available human fossils assigned to UP assemblages has led to the revision of the antiquity of a number of specimens and has fueled the notion that the producers of the earliest phases of the Aurignacian are actually unknown (e.g., Conard et al., 2004). Yet the direct dating of the available fossil record has also confirmed the EUP age of a series of early UP human remains. Significant human remains are still yet to be found from the proto-Aurignacian, which developed in Southern Europe in parallel to the Early Aurignacian prevailing north of the Alps. However, in Western Europe indisputable modern human remains have been identified in Early Aurignacian archeological

contexts at La Quina-Aval and Brassempouy (France). For the period from 35 to 28 ka ^{14}C BP (ca. 36.5–35 kcal BP), seven rather complete skulls are documented in Europe. They have mostly been found out of firmly established archaeological contexts; however, it is difficult to conceive what other assemblages besides one or another variant of the Aurignacian these humans may have produced. Fossils such as those from Mladeč provide us with a rather precise picture of the skeletal features of these populations. Farther east, the remains from Peștera cu Oase demonstrate the occurrence of modern humans already ca. 35 ka ^{14}C BP (ca. 40 kcal BP). It has been proposed that the Peștera cu Oase MH could have been the makers of “transitional” assemblages such as the Bohunician (Stringer, 2011). This is unlikely as these assemblages appear to be older when they are geologically dated in stratified open-air sites. Furthermore, the TL dating of the Bohunician layers at Brno-Bohunice provides a weighted mean of 48.2 ± 1.9 kcal BP for eleven heated flint samples (Richter et al., 2008). In ^{14}C chronology, this would predate the oldest date at Peștera cu Oase by ca. 10 ka. It is most likely that the modern humans from Peștera cu Oase utilized an Early Aurignacian or a proto-Aurignacian industry.

The scarcity of Aurignacian human remains found in well-established archaeological contexts may result from peculiar funerary customs, contrasting with the primary burials found in the MP and in the later UP. As already noted (Henry-Gambier and White, 2006; Henry-Gambier and Sacchi, 2008), the Aurignacians seemed to have a special interest in the postmortem manipulation of human remains. At Les Rois, La Crouzade, Brassempouy, La Combe, and possibly Isturitz, cutmarks and scrapes have been found on human remains or sometimes pierced human teeth. The deposit of bodies in the depths of karstic cavities or some varieties of secondary burials, with or without artifacts, may also explain some patterns observed in the fossil record. If proven to be associated with this technocomplex, the occurrence of a burial at Kostenki 14 would indicate, however, that primary inhumation was at least occasionally practiced at the easternmost extension of the Aurignacian domain.

Contrary to a commonplace opinion, the dental material yielded by EUP sites can be used to identify the occurrence of modern humans when it is dealt with in an appropriate manner. Although the polarity of non-metrical dental features is not always easy to establish (Bailey et al., 2011), when sufficient material is available these features allow for distinguishing between Neandertals and MH. They complete the limited evidence provided by the classic metrical approaches. Incorporating all of the available material leads to the conclusion that there is no positive evidence of the occurrence of Neandertals in any well-established Aurignacian context to date (Bailey et al., 2009). Although the theory can be considered, the possibility of such an occurrence remains purely speculative. Although AMS dates ca. 33–32 ka ^{14}C BP (ca. 37.5–36.5 kcal BP) have been obtained on Neandertal remains from layer G1 of Vindija cave, Croatia (Higham et al., 2006), the association of these remains with an Aurignacian style split-based bone point is highly questionable (Kozłowski, 1996; d’Errico et al., 1998). Direct dating of faunal remains from this layer, as well as the refitting of stone artifacts from different layers of Vindija, also suggests vertical admixture in the site (Bruner, 2011). The fragmentary specimen of Les Rois B represents an even more tenuous piece of evidence. In the end, when one takes into account all of the human remains found in Europe that can safely be assigned to the period between 35 and 28 ka ^{14}C BP (40–32 kcal BP), it is difficult to argue that the artisans of the Aurignacian, including in its older phase, were not modern humans.

The transitional assemblages provide us with a more complex pattern (see Figures 6.5 and 6.6). The most parsimonious explanation for the association of Neandertal remains with Châtelperronian assemblages in Arcy-sur-Cure and Saint-Césaire is that these hominins were the makers of the lithic and bone industries in these sites. The geographic distribution of the Châtelperronian, closely fitting that of the MTA-B, is another argument supporting direct cultural and biological continuity between at least one local MP assemblage and one

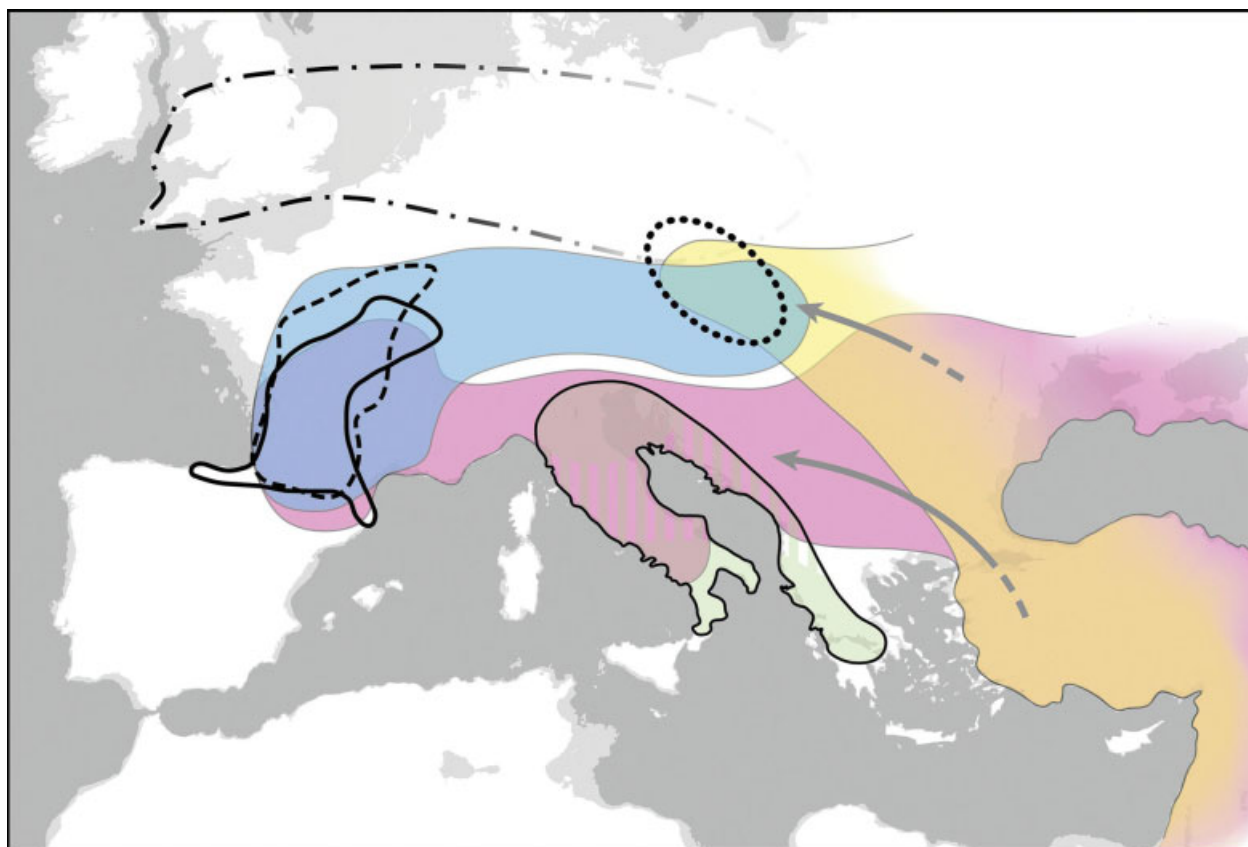


Figure 6.5. Geographical distributions of the main lithic assemblages of Western Eurasia between 50 and 35 ka cal BP. With the exception of the MTA, the late Mousterians are not represented. Colored areas represent assemblages tentatively assigned to modern humans and areas limited by thick black lines are tentatively assigned to late Neandertals. Emirian/Bachokirian/Bohunician, Early Ahmarian/Kozarnikian/Protoaurignacian, Early Aurignacian, Uluzzian, Szeletian, - - - - MTA, ——— Châtelperronian, — · - LRJ. For color detail, please see color plate section.

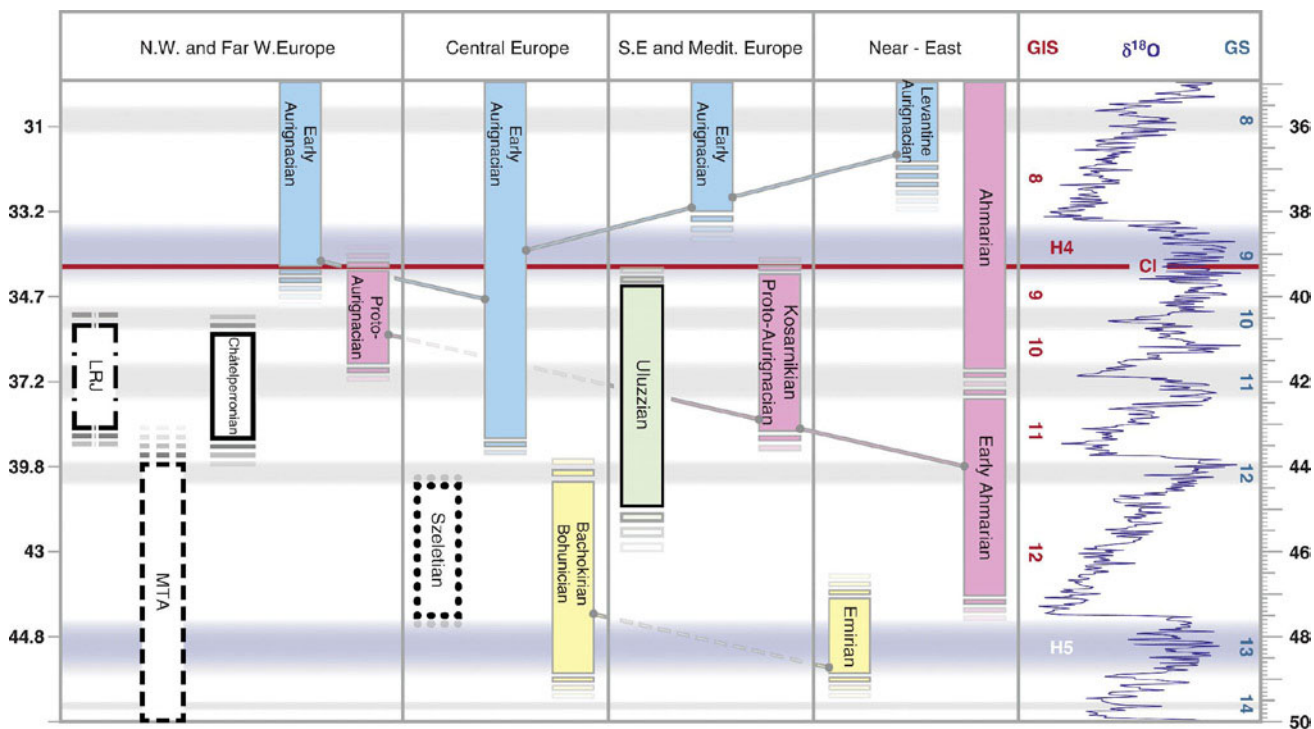


Figure 6.6. Tentative chronological distribution of the assemblages listed in Figure 6.5. The timescale on the right side is calibrated and the timescale on the left side provides an approximate equivalent in ^{14}C chronology (Bronk Ramsey, 2009; Reimer et al., 2009). The curve of the $\delta^{18}\text{O}$ variations in the North Greenland Ice-Core Project (NGRIP) is from <http://www.gfz.ku.dk/~www-glac/data/gripdelta.dat>. Gray horizontal bands indicate cold stadials (GS), and the white horizontal bands indicate the interstadial periods (GIS). Heinrich Events 4 (H4) and 5 (H5) are indicated in blue and the time of the mega-eruption of the Campanian Ignimbrite (CI) is indicated by a red line. For color detail, please see color plate section.

transitional assemblage in Western Europe. However, the notion that part of the transitional assemblages was actually produced by modern humans predating the Early Aurignacian has recently found some support through the reexamination of the fragmentary human remains found in Uluzzian contexts in Italy. These dental remains have been identified as modern, pushing back the first occurrence of MH in Europe to between 45 and 43 ka calendar years ago (Benazzi et al., 2011). A similarly old occurrence of modern humans in Western Europe has been claimed based on the reinvestigation around the Kent's Cavern (UK) maxilla. This fragmentary specimen (Kc4) was directly dated at $30,900 \pm 900$ ^{14}C BP (36.4–34.7 ka cal BP) (Hedges et al., 1989). However, Higham et al. (2011b) argued that this age is a strong underestimate. The dating of faunal elements from the sector from which the specimen comes led them to propose an age between 44.2 and 41.5 ka cal BP for the maxilla. Furthermore, out of twenty-three dental traits examined on the specimen, thirteen possess MH rather than Neandertal affinities. However, it should be underlined that this study does not provide any new direct dating of the Kc4 specimen and that the integrity of the stratigraphic section in the part of Kent's Cavern where the human fossil was discovered in 1927 is debated (Pettitt and White, 2012). Another issue related to the interpretation of the Kc4 specimen relates to the fact that with an age between 44.2 and 41.5 ka cal BP, this allegedly modern specimen would become a candidate for the production of the LRJ in the British Islands. This contradicts the Neandertal nature of the LRJ that has often been assumed and that has been deduced from the dating of the Spy specimens (Semal et al., 2009). Similarly, current scenarios explaining the emergence of the Uluzzian industry in a rather restricted region are hardly compatible with its assignment to modern makers.

In Central Europe, a rather different picture emerges. In this area so-called “transitional assemblages,” as well as “initial UP,” have not yet yielded any human remains. For the Bohunician, this situation primarily results from taphonomical reasons. This assemblage is normally found inside the Bohunice soil, which is strongly acidic, and thus there are no bones at any of the open-air sites. It is, however, likely that at least some of the “transitional assemblages” from this area that far predate the Early Aurignacian, such as the Bohunician and the Bachokirian, may have been produced by modern humans. Their mixed technological features, including the persistence of Levallois or Levallois-inspired techniques, would not result from any local continuity but rather from their rooting in MP/MSA technical traditions outside of Central Europe. They are quite reminiscent of assemblages known in the Near East. This correlation has been made in particular for the Bohunician, which displays a knapping technique quite different from the local Mousterian tool production (Svoboda, 2005) but shares similarities with the Levantine Emirian assemblage (Bar-Yosef, 2003, 2007; Hoffecker, 2009; Tostevin, 2003). In contrast, the contemporary Szeletian seems to be locally rooted in the eastern Micoquian Neandertal production of foliate points (Nigst, 2012).

Later in time, a growing number of authors also connect the proto-Aurignacian and its Eastern European expression (e.g., Kozarnikian) to assemblages found farther east in Eurasia and all characterized by the spectacular development of the production of large bladelets likely related to the development of light missile weapons (Le Brun-Ricalens et al., 2009). The early stages of the Ahmarian in the Near East is seen as the most likely origin of the European proto-Aurignacian (Bar-Yosef, 2007). The later Ahmarian layer XVII of Ksar-Akil, Lebanon, yielded the remains of a child aged between 7 and 9 years by modern standards. Although this specimen can only be studied through casts, it is unequivocally modern (Bergman and Stringer, 1989).

This emerging model of the arrival of MH in Europe prior to the Aurignacian has been tentatively connected to the spectacular environmental changes witnessed during MIS 3. To start, it is quite unlikely that the colonization of Europe by MH could have been triggered by the environmental hazard of the mega-eruption of the Campanian Ignimbrite or the

Heinrich 4 event that would have emptied large portions of Europe of its Neandertal populations. As a matter of fact, the Early Aurignacian and proto-Aurignacian themselves are documented in Central and Mediterranean Europe before these events, and proto-Aurignacian has been found in stratigraphy under the CI tephras in Italy (Giaccio, 2005; Lowe et al. 2012). Müller et al. (2011) rather argue that the very first arrival of MH in Europe may already have occurred under the mild conditions of the GIS 14–13 that, according to the TL dates in Bohunice (Richter et al., 2009), could have witnessed the beginning of the Bohunician. Later, the Heinrich event H5 represented a major climatic deterioration ca. 48 ka ago, as extreme as the glacial maximum of the MIS 4 when large portions of Europe were abandoned by Neandertals. Although to date there is only minimal evidence of an intense cold peak at this time recorded in the middle and lower Danubian loess (Stevens et al., 2011), most likely the Heinrich H5 event also created a demographic vacuum in large portions of Europe that later facilitated the expansion of MH from southern refuges during GIS 12 ca. 47 kcal BP. This period witnessed the rapid shift from desert-steppe to open woodlands in eastern Mediterranean regions. The following Heinrich event (H4) may have delayed the expansion of MH only in some parts of Western Europe, as proposed by Sepulchre et al. (2007) for the Iberian peninsula, where it boosted aridity and where a late survival of the Neandertals is inferred from the archaeological record.

The arrival of MH in Europe prior to the dawn of the Aurignacian and a stepwise model for the colonization of some parts of the continent has important implications regarding the biological and cultural evolution of MH and late Neandertals in the area and regarding the possible interactions between the two groups. It brings strong support to the acculturation models for the explanation of the late Neandertal techno-cultural evolution (Hublin et al., 1996, 2012a; Nigst, 2012; Roussel, 2011; Tostevin, 2000) and invalidates the chronological and stratigraphic arguments alternatively supporting a local and independent invention of the UP by the last Neandertals (Zilhão and d’Errico, 2000). Interestingly, this early diffusion of new behaviors within the Neandertal population could not only explain the patterns observed in so-called “transitional assemblages” such as the Châtelperronian but also the cultural changes observed in some late Mousterians themselves, such as in the MTA, which, among other features, display a development of the use of oxides often referred to as “pigments” (Demars, 1992). In some cases (e.g., Szeletian) the influence of the modern newcomers likely exerted at short distance, in other situations (MTA, Châtelperronian, LJR) it likely resulted from diffusion within late Neandertal groups at distance from the initial contact zones.

In the biological record, the persistence of “archaic” traits, rare in recent modern populations, has also been the object of contrasting interpretation. As for the MP technical features observed in transitional assemblages, the first explanation to be provided for the persistence of these traits is through some kind of continuity between local Neandertals and EUP MH. Although the notion of a simple *in situ* evolution has mostly been abandoned, a more or less intense level of gene flow between the two groups has been assumed by some (Zilhão, 2006). If such gene flow is not unlikely to have occurred at the time of the replacement of the Neandertal populations, it is difficult to demonstrate in the fossil record remains, and overall its magnitude remains debated. One problem in interpreting the fossil material of the EUP results from the confusion existing in the literature between “archaic” and “Neandertal” features. To date it has been impossible to identify the occurrence of truly unique Neandertal features among the MH of the EUP in Europe, as most of the discussed features can be observed at least in some frequency, or with a different pattern, in MH populations inside and outside of Europe. The geometry of the frontal squama of Hahnöfersand (Bräuer, 1980), the Neandertal-like horizontal-oval shape of the mandibular foramen, the rather vertical mandibular symphysis and the small retromolar space of the Stetten/Volgelherd 1 mandible (Freyer et al., 1993; Smith, 1984) were once highlighted as being

the result of hybridization processes between Neandertals and MH in the EUP. These two specimens have in fact since been demonstrated to be from the Holocene.

The anatomical features supposed to bring some support to the assimilation model can alternatively be interpreted as archaic features inherited not from the European Neandertals but from earlier non-European forms of MH. In this respect the comparison with North African human fossils predating 40ka is illuminating. For example, the proportions of the molar series and some non-metrical dental features visible on the specimens of Peștera cu Oase, which have been claimed to be Neandertal-like, can also be observed on Aterian remains from Northwestern Africa (Hublin et al., 2012b). This is also true for the vertical orientation of the mandibular symphysis. On Nazlet Khater 2, an EUP MH from Egypt, one also finds the broad mandibular ramus, the weak convexity of the frontal and the anterior position of the zygomatics, as observed at Peștera cu Oase (Crevecoeur and Trinkaus, 2004; Rougier et al., 2007). This should at least encourage some caution when these features are interpreted as having a specific Neandertal source.

Although the study of mitochondrial DNA did not bring much support to the hypothesis of massive admixture between the two groups (Currat and Excoffier, 2004), the sequencing of the Neandertal nuclear genome showed that a small amount of Neandertal genetic material can be identified in non-African modern humans (Green et al., 2010). To date, the genetic data do not indicate that this introgression was especially strong in Europe, where Neandertal populations are best documented. The ubiquity of this trace at a low level throughout Eurasia, including in Asian regions where Neandertals never lived, instead suggests that this gene flow occurred before or at the very beginning of the dispersal of MH throughout Eurasia, and before they witnessed a large demographic development. If one takes into account the small effective population for the non-African extant humans, this phenomenon may in fact have initially implied a very limited number of individuals in the Near East. To reconcile a much larger level of admixture between Neandertal populations and MH invaders in Europe with the average 2.5% of genetic material of Neandertal origin observed in extant MH of Western Eurasia one should envision that, at least in some parts of Europe, EUP MH once displayed a much higher percentage of this material but were subsequently replaced by other human groups. The ongoing paleogenetic investigation on MH from the UP will hopefully shed some light on this issue.

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Note

1. Calibrated dates in this paper are generated using the InCal09 and OxCal4.1 programs (Bronk Ramsey, 2009; Reimer et al., 2009).

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Chapter 7

Neandertal Craniofacial Growth and Development and Its Relevance for Modern Human Origins

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Introduction

The first Neandertal ever discovered consisted of the remains of a young child, Engis 2, found in a cave near Liège, Belgium, in 1829 (Fraipont, 1936; Tillier, 1983). The assemblage includes an immature calvarium and an isolated facial fragment containing a full complement of deciduous teeth and a large crypt for M¹. Since this older infant lacked adult characteristics, its significance was not understood until the early twentieth century (Fraipont, 1936; Tillier, 1983; Minugh-Purvis, 1988). Additional immature Neandertal fossils have since been discovered, providing the most well-represented record for non-adults among fossil hominins. Analyses comparing Neandertal and modern human adults have dominated the literature on modern human evolution (see, e.g., Boule, 1912; Hrdlička, 1927; Keith, 1931; Vallois, 1954; Howell, 1957; Boule and Vallois, 1959; Brace, 1962, 1964; Howells, 1967; Wolpoff, 1968, 1986; Smith, 1984; Rak, 1986; Demes, 1987; Trinkaus, 1987; Stringer and Andrews, 1988; Bräuer, 1989; Smith et al., 1989; Comdemi, 1991; Bräuer and Smith, 1992; Trinkaus and Shipman, 1992; Frayer et al., 1993; Stringer and Gamble, 1993; Smith, 1994; Franciscus and Trinkaus, 1995; Wolpoff and Caspari, 1997; Dobson and Trinkaus, 2002; Trinkaus, 2003; Harvati 2003; Harvati et al., 2004; Ackermann, 2005; Trinkaus, 2006, 2007). Some descriptive accounts of juvenile Upper Pleistocene fossils also exist (e.g., Martin, 1926; Garrod et al., 1928; Fraipont, 1936; Heim, 1982; Tillier, 1982, 1983; Dodo et al., 1998; David et al., 2009; Toussaint et al., 2010). The postnatal ontogenetic patterns of Neandertals and modern humans have been less often addressed (Skinner, 1978; Tillier, 1983, 1989; Dean et al., 1986; Minugh-Purvis, 1988; Stringer et al., 1990; Tompkins, 1996; Williams, 2000; Ponce de León and Zollikofer, 2001; Williams et al., 2002, 2003; Williams and Krovitz, 2004; Williams, 2006; Ponce de León et al., 2008; Glantz et al., 2009; Gunz et al., 2010; Cowgill, 2010).

Approximately half of the sixty (minimum) immature Neandertal fossils are well preserved (Tillier, 1982, 1983, 1989, 1995; Minugh-Purvis, 1988; Dodo et al., 1998; Williams et al., 2002, 2003). The earliest stages of Neandertal craniofacial ontogeny are particularly difficult to assess, as all the fetal, neonatal, and young infant Neandertal remains are extremely

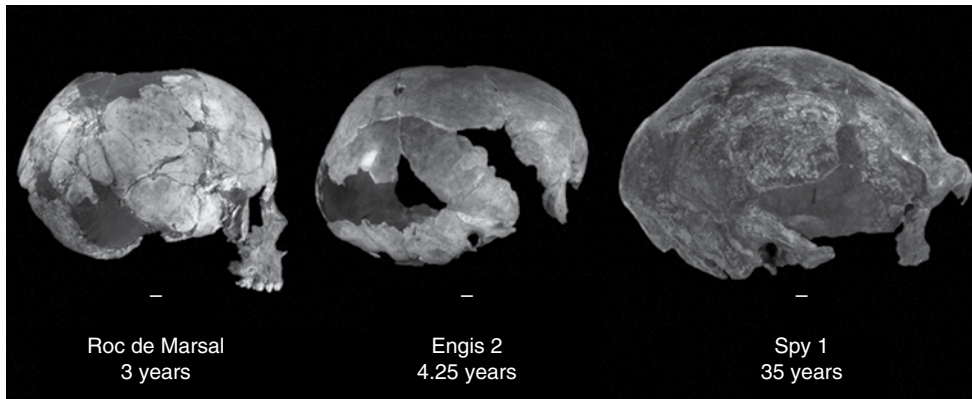


Figure 7.1. Roc de Marsal, Engis 2, and Spy 1 (lateral views). Photographs of Roc de Marsal (3 years), Engis 2 (4.25 years), and Spy 1 (35 years) are juxtaposed to exemplify the marked differences in craniofacial shape that occurred during the Neandertal life cycle. The three are shown with scale bars equal to 1 cm. The cranium of Roc de Marsal is oriented both posteriorly and superiorly to the face. The face is orthogonal, although the nasal bones extend anteriorly. The occipital region is somewhat angled, suggestive of an incipient occipital torus. The supraorbital region shows only a very slight relief. In Engis 2 the neurocranium is also oriented posteriorly with respect to the face, with a moderately vertical anterior frontal squama. The supraorbital torus is well defined with respect to this life cycle stage, but not to the extent to which it is present in adults, such as Spy 1. In Spy 1 the supraorbital torus is large and arched and protrudes anteriorly. A low frontal squama emerges behind the massive browridges. The cranial vault is oriented posteriorly, and a prominent occiput is present. Although some Neandertal traits can be identified early in postnatal ontogeny, profound differences in cranial form are clearly apparent between Neandertal children and adults, suggesting fundamental changes in shape accrued during the juvenile and subadult maturational phases.

fragmentary (Tillier, 1989), although the relatively complete remains of a neonate, Le Moustier 2, imply greater similarities with Neandertal adults compared to infant modern humans, at least craniodentally (Maureille, 2002). However, for the most well-preserved neonatal material aged from birth to 7–9 months (e.g., La Ferrassie 4/4bis¹ and 5, L'Hortus 1 and 1b, Shanidar 7 and 9, and Kebara 1), “not even a single complete bone can be scientifically reconstructed” (Tillier, 1995: 64). Ponce de León et al. (2008) simulated the birth of Mezmaiskaya, a relatively complete but fragmentary neonatal cranial vault, from the Tabūn C1 pelvis and suggested that parturition and brain size at birth in Neandertals fell within the range for modern humans. The remains of older infants, including those with complete sets of deciduous dentition prior to the eruption of M1 (Subalyuk 2, Pech de l’Azé, Roc de Marsal, Archi 1, Engis 2, Devil’s Tower [Gibraltar 2], and Dederiyeh 1 and 2) and individuals with a mixed dentition or unerupted teeth (La Quina 18, Teshik-Tash 1, Sclayn, Krapina Maxillae B, C, D, E and Mandibles C, D, E, F, G, H, J, and Malarnaud and Le Moustier 1) are much more complete than the neonatal and early infant stages. From this assemblage, craniofacial changes from late infancy to adulthood in Neandertals can be reconstructed (Figure 7.1).

Neandertal and Modern Human Rates of Craniofacial Ontogeny

It has been suggested that Neandertals and modern humans show distinct developmental trajectories from birth, or even prenatally, to adulthood (e.g., Green and Smith, 1990; Graves, 1991). Differences between the two adults would be expected to occur

early in ontogeny (Cartmill and Smith, 2009). Craniofacial distinctions such as sphenoid shortening have been utilized to claim that Neandertals and modern humans are different species (cf. Lieberman, 1998; Spoor et al., 1999). In opposition, Vlcek (1964) asserted that adult features of Neandertals do not exist in the neonatal period, but in contrast arise between 2 years and adulthood. Upon examination of L'Hortus 1 and 1B and other young infant remains De Lumley (1973) and Tillier (1989) also found a lack of typical adult traits manifested early in the postnatal development of Neandertals. Trinkaus (1983) observed an overall absence of adult Neandertals features in Shanidar 7. A slightly raised supraorbital torus was noted for some neonates such as La Ferrassie 4b, and fetal material such as La Ferrassie 5 (Heim, 1982; Minugh-Purvis, 1988). Partial development of traits typical of Neandertal adult traits have been also been noted, such as the manifestation of unique aspects of occipital form and the morphology of the glenoid fossa of the temporomandibular joint in La Ferrassie 8, as well as a slight vertical angulation of the temporal squama in Subalyuk 2 (Minugh-Purvis, 1988). Ponce de León and Zollikofer (2001) argued that Neandertal traits emerged early, possibly during gestation, as extrapolated from older infants such as Pech de l'Azé and Roc de Marsal. Coqueugniot and Minugh-Purvis (2003) noted that mental foramen position vis-à-vis the tooth under which it occurs differs significantly between Neandertals and modern humans even at early postnatal ages. Tillier (1982, 1983, 1989) identified the development of several neurocranial features characterizing Neandertal adults on young individuals greater than 2 years, but she suggested that other adult traits arise later in conjunction with the emergence of the permanent teeth and the expansion of the nasal apparatus (Tillier, 1989, 1995).

Bolk (1926) was the first to suggest that the expression of Neandertal adult features resulted from faster rates of absolute growth. Brothwell (1975) posited that distinct endocrine profiles characterized Neandertals resulting in an acceleration of growth before puberty beyond that exhibited by modern humans. He suggested that such an endocrine change was an adaptation to the extreme cold weather conditions prevalent during the Upper Pleistocene. An examination of Le Moustier 1 led Thompson and Illerhaus (1998) to conclude that this subadult had experienced accelerated growth of the height of the face with respect to prognathism. Williams (2000) identified an acceleration of masticatory growth in Neandertals compared to modern humans. Dean et al. (1986) and Stringer et al. (1990) suggested that Neandertals exhibited a relatively fast rate of neurocranial growth compared to dental development from a tallying of incisal perikymata in Devil's Tower (Gibraltar 2). However, these results were based on a single tooth (Tillier, 1995).

Legoux (1966) observed an acceleration of crown calcification and a rapid eruption of the dentition in Neandertals compared to modern humans. Similarly, Wolpoff (1979) argued that Neandertals erupted M3 earlier (15 years) compared to modern humans based on the attrition rates of the molars. Furthermore, Tompkins (1996) found a faster calcification of M3 in Neandertals compared to modern humans. However, he noted a greater similarity between Neandertals and early modern humans in dental eruption patterns with respect to recent modern human groups. Tompkins (1996) also observed that both Neandertals and early modern humans could be characterized by their relatively rapid calcification of M2 compared to modern human groups. Reinforcing the argument, Bayle et al. (2009) found the patterns of crown calcification in early modern humans, from the Gravettian-Solutrean strata (Abrigo do Lagar Velho) to late Pleistocene Magdalenian layers (La Madeleine 4), to resemble those of Neandertals more than those of extant humans. In contrast, a rapid ontogenetic development in Neandertals was proposed by Ramirez Rozzi and Bermúdez de Castro (2004), who, on the basis of perikymata counts, suggested that Neandertals reached maturation at 15 years. This position was refuted by Macchiarelli et al. (2006) who found

insignificant differences in the rates of Neandertal and modern human tooth formation when large samples of modern humans are included, although the authors found that Neandertals are distinct in enamel-dentine junction form and the protracted rate of molar root expansion. From an investigation of the Sclayn juvenile from Belgium (Smith et al., 2007) and the Lakonis molar from Greece (Smith et al., 2009), it was suggested that molar calcification times were faster in Neandertals than those typical of modern humans, whereas Guatelli-Steinberg and Reid (2008) and Reid et al. (2008) argue that the fundamental patterns of dental development in Neandertals and modern humans are not distinct. Additional support for a correspondence between Upper Pleistocene and modern human life cycles derives from Ponce de León et al. (2008), who suggest that large brain size in both adult and neonatal Neandertals would have required late-maturing mothers. The inference is that Neandertal and modern human life histories would have to be profoundly similar and were probably inherited from a common ancestor.

The pronounced occiput characterizing Neandertal adults was proposed to derive from a continuation of growth in the occipital region beyond the juvenile period to account for the pronounced occiput of adults (Trinkaus and LeMay, 1982). Similarly, the premaxillary suture tends to persist in Neandertal juveniles longer than is the case in modern humans, perhaps signally a longer period of facial growth (Maureille and Bar, 1999). Multivariate analyses of gnathic remains from Krapina led Williams (2006) to suggest that dimensions of the face typical of Neandertal adults are not found among infants and juveniles, and therefore must have been greatly amplified between the eruption of the second and third molars.

Other researchers have contrasted Neandertal and modern human cranial growth. In a study of Neandertal and modern human infant, juvenile and adult brain sizes, Trinkaus and Tompkins (1990) noted that Neandertals are found within one to two standard deviations of modern humans. Skinner (1978) observed similarities in cranial growth, and to a lesser degree, facial growth among Upper Paleolithic and recent human groups. However, Neandertals were distinct by exhibiting upper and lower facial regions that were larger throughout the life cycle (Skinner, 1978). Minugh-Purvis (1988) noted rate differences in facial growth when Neandertals and modern humans were compared, but she posited that Skhül, Qafzeh and European Upper Paleolithic humans were strikingly more similar in their patterns of craniofacial ontogeny to Neandertals than they were to modern humans.

Neandertal and Modern Human Rates of Shape Change

A number of researchers have explored rates and patterns of shape change to account for the differences observed between adult Neandertals and modern humans (Krovitz, 2000; Williams, 2000, 2001, 2006; Ponce de León and Zollikofer, 2001; Williams et al., 2002, 2003). Krovitz (2000, 2003) digitized cranial landmarks on ontogenetic series of Neandertals and modern humans and, utilizing Euclidean Distance Matrix Analysis (Lele and Richtsmeier, 1991; Richtsmeier et al., 1993; Richtsmeier and Walker, 1993), showed that the magnitude of difference between the two taxa increases as a function of time during postnatal ontogeny. Williams et al. (2002) contrasted Neandertal and modern human ontogenetic sequences and found that a simple extrapolation of common patterns of shape change cannot explain the differences between adults of the two taxa. Williams (2001) observed that the calvarium of Neandertals can be described as “paedomorphic” or juvenilized with respect to the overall shape of modern human adult cranial vaults because Neandertals maintain a posterior orientation of the calvarium typical of infant *Homo* into

adulthood. In contrast, modern human infant calvaria, which are oriented posteriorly during infancy, change markedly around the eruption of the first molar (or earlier; see Gunz et al., 2010) coinciding with the beginning of the juvenile life cycle stage. However, Neandertals, compared to modern humans, experienced a greater intensity of orbital and masticatory shape change during postnatal ontogeny (Williams, 2001).

Zollikofer and Ponce de León (2010) incorporated Neandertal ontogeny into a general model of hominin development demonstrating the importance of Late Pleistocene populations to understanding the unique aspects of modern human life history and human behavioral ecology. Arising from the conceptual models of Gould (1977), and furthered by the work of Godfrey and Sutherland (1995a, 1995b, 1996), researchers have sought to evaluate the predictions of neoteny with respect to human ontogeny and phylogeny. Tillier (1995), Williams (1997), and Churchill (1998) positioned Neandertals directly within the context of heterochrony and human evolution. Later authors (Williams et al., 2002, 2003; Williams and Krovitz, 2004) tested the predictions of neoteny with respect to Neandertal and modern human postnatal ontogenetic trajectories. Although modern humans exhibit weaker growth allometries (a prediction of neoteny) with respect to Neandertals, the two follow different shape paths (Williams et al., 2002). When Neandertals are modeled as ancestors and modern humans are modeled as descendants, global neoteny fails as a description of modern human craniofacial form; modern human adults are primarily smaller than Neandertal adults, and several heterochronic processes would have to be invoked, along with neomorphy, to account for modern human adult craniofacial shape arising from a Neandertal-like ancestor (Williams et al., 2003).

Furthermore, heterochrony alone cannot account for the differences in mental foramen position between Neandertals and modern humans. In a study of Neandertal and modern human mental foramen position during postnatal ontogeny, Williams and Krovitz (2004) examined whether the two taxa share the same mandibular shape path from infancy to adulthood, and if so whether the differences between the adults can be described in a heterochronic framework. They found that the mental foramen may appear to be more anteriorly positioned in modern humans because Neandertals often exhibit mesiodistally short premolars coupled with a relatively large mandible when compared to extant *Homo*. The two taxa exhibit a similar placement of the mental foramen throughout postnatal ontogeny when mandibular size is considered, and thus modern humans cannot be described as neotenes (or juvenilized) in the position of the mental foramen (Williams and Krovitz, 2004).

Given the debate on rates of growth and their bearing on life history, whether Neandertals exhibit accelerated or decelerated craniofacial rates of growth and maturation compared to modern humans is explored here. Understanding the range of variation of Neandertal postnatal growth, the rate and duration of growth, and when adult traits appear has been stymied by the lack of large numbers of relatively complete infants, juveniles, subadults, and adults. To compensate for the limited ontogenetic sequence available for the fossils, growth trajectories are approximated by non-linear modeling. Most Neandertal non-adults are represented solely by fragmentary calvaria, maxillae, and/or mandibles constraining the present study to modeled growth patterns of the cranial vault, face, and mandible. These patterns of growth will be utilized to infer growth rates and ages at maturation for those craniofacial dimensions most often preserved in Neandertals. A further goal is to examine the degree of multivariate shape change from infants to adults in craniofacial proportions. The two species of *Pan* provide an analogue upon which to benchmark the differences observed in Neandertals and modern humans. Whether the postnatal ontogenetic differences between Neandertals and modern humans exceed those found between the two species of *Pan* is also addressed.

Materials and Methods

Neandertal Sample

Measurements on original Neandertal fossils ($n = 39$) and two casts (Teshik-Tash 1 and Šipka) were collected at institutions in Europe and Israel. These Neandertals are located at museums in Belgium (Institut Royal des Sciences Naturelles de Belgique, Brussels, Université de Liège, and the Direction de l'Archéologie, Ministère de la Région Wallonne), Croatia (Croatian Natural History Museum), the Czech Republic (Moravské Muzeum), France (Musée de l'Homme, Musée des Antiquités Nationales, Saint Germain-en-Laye, Musée National de Préhistoire, Les Eyzies-de-Tayac, and the Université de Poitiers), Hungary (Természettudományi Muzeum), Israel (Tel Aviv University), Italy (Museo Preistorico Ethnografico "Luigi Pigorini" and the Istituto di Paleontologia Umana), and the United Kingdom (Natural History Museum). Of the total number of forty-one individuals, sixteen are in reasonable to excellent condition and degree of preservation, while twenty-five consist of either maxillary or mandibular elements. One specimen, Šipka, is represented by a primary cast, the actual fossil having been destroyed in a fire (Minugh-Purvis, 1988). Table 7.1 shows a listing of the Neandertal sample by estimated dental age and state of completeness. The relatively complete calvarium and mandible of Le Moustier 1, a subadult aged to 16.5 years (Minugh-Purvis, 1988), was not considered because this specimen was unavailable during the data collection phase of this study.

Modern Human Sample

The modern human sample ($n = 294$) derives from institutions in Belgium (Institut Royal des Sciences Naturelles de Belgique), the Netherlands (Vakgroep Anatomie en Embryologie and the Anatomisch Museum, Rijksuniversiteit Groningen; Centrum voor Fysische Antropologie and the Anatomie Museum, Rijksuniversiteit Leiden, the Nationaal Natuurhistorisch Museum, and Rijksdienst voor Oudheidkundig Bodemonderzoek), and the United States (American Museum of Natural History and Johns Hopkins University School of Medicine, Baltimore). All specimens were selected from museum collections on the basis of preservation (crania without mandibles and/or partially destroyed were excluded) and age. Skulls of advanced age showing marked alveolar resorption and/or considerable postmaturational cranial vault remodeling, were excluded to avoid incorporating shape changes associated with maturational decline.

The modern human sample includes individuals from archaeological, historical, and recent populations from a variety of geographical locations. Many individuals are from Europe ($n = 63$); others originate from Southeast Asia ($n = 18$), the Americas ($n = 20$), Southwest Asia ($n = 11$), sub-Saharan Africa ($n = 14$), and Papua New Guinea ($n = 24$). An archaeological sample from Belgium ($n = 54$) included remains from Coxyde (or Koksijde), a twelfth- to seventeenth-century Flemish monastery population, and from Achet, a fourth- to eighth-century Merovingian site. Eight additional adults, and three collections of infants and children with no locality information ($n = 90$), were also utilized. The total modern human sample comprises thirty-two fetuses, neonates, and very young infants less than 6 months of age, eighteen infants between 6 months and 2.4 years, and forty-seven older infants between the ages of 2.5 and 5.5 years. Most of these young individuals are currently located at the Rijksuniversiteit Leiden, the Rijksuniversiteit Groningen, and the Pennsylvania State University (the Bosma collection, formerly at Johns Hopkins University). The modern

Table 7.1. Age at death, life cycle stage, and preservation of Neandertal fossils.

Individual	Age	Preservation
Amud 7	0.45	Partial cranium, mandible ¹
Subalyuk 2	2.5	Neurocranium, palatal fragment ²
Pech de l'Azé	2.75	Relatively complete cranium ³
Châteauneuf-sur-Charente 1	3	Mandibular corpus ³
Roc de Marsal	3	Nearly complete skull ⁴
Archi 1	3.5	Mandible ⁵
Engis 2	4.25	Neurocranium, palatal fragment ⁶
Devil's Tower 2 (Gibraltar 2)	4.75	Cranial bones, partial mandible ⁷
Krapina Maxilla B	6	Maxillary fragment ⁸
La Quina 18	7.5	Nearly complete cranium ⁹
Teshik-Tash 1	9.5	Nearly complete skull (cast) ¹⁰
Krapina Maxilla C	9.5	Maxillary fragment ⁸
Šipka	10	Mandibular fragment (cast) ¹¹
Sclayn	11	Mandible, maxillary fragment ¹²
Krapina Mandible C	11	Mandibular fragment ⁸
Krapina Mandible E	14	Mandibular fragment ⁸
Krapina Mandible F	15	Mandibular fragment ⁸
Krapina Mandible D	15	Mandibular fragment ⁸
Krapina Maxilla D	15.5	Maxillary fragment ⁸
Malarnaud	16	Partial mandible ¹³
La Naulette	17.5	Partial mandible ¹⁴
Krapina Mandible G	18	Mandibular fragment ⁸
Monte Circeo III	19	Partial mandible ¹⁵
Krapina C3	19	Partial neurocranium ⁸
Krapina Ramus 66	20	Ascending ramus ⁸
Krapina Ramus 63	20	Ascending ramus ⁸
Krapina Mandible J	21	Nearly complete mandible ⁸
Ochoz	21	Partial mandible ¹⁶
Subalyuk 1	22	Partial mandible ²
La Ferrassie 1	25	Nearly complete skull ¹⁷
Forbes' Quarry (Gibraltar 1)	25	Partial cranium ¹⁸
Tabūn C1	25	Calvarium, lower maxilla, mandible ¹⁹
La Quina H5	25	Calvarium, lower maxilla, mandible ⁹
Spy 2	25	Calvarium, lower maxilla, mandible ²⁰
Kebara 2	30	Nearly complete mandible ²¹
Amud 1	30	Nearly complete skull ¹
Krapina Mandible H	32	Partial mandible ⁸
Spy 1	35	Calvarium, lower maxilla, mandible ²⁰

(Continued)

Table 7.1. (Continued)

Individual	Age	Preservation
Monte Circeo II	42	Partial mandible ²²
Guattari 1 (Monte Circeo 1)	42	Nearly complete cranium ²³
La Chapelle-aux-Saints	45	Nearly complete skull ²⁴

¹Suzuki and Takai (1970), Rak et al. (1994); ²Bartucz and Szabó (1940); ³Patte (1957); ⁴Bordes and LaFille (1962), Madre-Dupouy (1976), Turq (1989); ⁵Ascenzi and Segre (1971); ⁶Schmerling (1833–1834), Fraipont (1936), Tillier (1983); ⁷Garrod et al. (1928); ⁸Gorjanović-Kramberger (1906), Radovčić et al. (1988); ⁹Martin (1911, 1920, 1926); ¹⁰Okladnikov (1940), Weidenreich (1945); ¹¹Maška (1882); ¹²Toussaint et al. (1998), Sclayn is aged at 8 years based on molar cuspal enamel formation times (Smith et al., 2007) but see Bayle et al. (2009); ¹³Petite-Marie et al. (1971); ¹⁴Dupont (1866), Leguebe and Toussaint (1988); ¹⁵Sergi and Ascenzi (1955); ¹⁶Rzehak (1905); ¹⁷Capitan and Peyrony (1909); ¹⁸Busk and Falconer (1865); ¹⁹Garrod and Bate (1937); ²⁰Fraipont and Lohest (1886), Semal et al. (2009); ²¹Bar-Yosef et al. (1986); ²²Sergi (1954); ²³Sergi (1939), Piperno and Scichilone (1991); ²⁴Boule (1911, 1912).

human sample additionally contains 48 juveniles between the ages of 6 and 11.5 years, 37 subadults between 12 and 17.5 years, and 112 adults over 18 years of age.

Pan troglodytes Sample

The *P. troglodytes* sample (n=156) was examined at the Powell-Cotton Museum, UK (n=86); the Nationaal Natuurhistorisch Museum, the Netherlands (n=32); the Anatomie Museum at the Rijksuniversiteit Leiden, the Netherlands (n=1); the Museum of Comparative Zoology at Harvard University (n=8); the Muséum National d'Histoire Naturelle, France (n=22); and the Koninklijk Museum voor Midden-Afrika, Belgium (n=7). Nine of these individuals were captive, whereas fifteen had no locality data. All other individuals were from West-Central and Central Africa, corresponding to *P. troglodytes troglodytes*.

Pan paniscus Sample

The *P. paniscus* sample (n=151) was largely obtained from the Koninklijk Museum voor Midden-Afrika, Belgium (n=146). Measurements on additional individuals were acquired from the Museum of Comparative Zoology at Harvard University (n=3), the Nationaal Natuurhistorisch Museum, the Netherlands (n=1), and the Muséum National d'Histoire Naturelle, France (n=1). One individual was captive, whereas the others were from Central Africa south of the Congo River.

Dental Aging

It is widely recognized that dental eruption patterns are the most accurate indicators of age in non-adults (Ubelaker, 1978; Cheverud, 1981; Richtsmeier et al., 1993; Buikstra and Ubelaker, 1994; Smith et al., 1994; Liversidge, 2003) because they are largely resistant to extrinsic insults (e.g., changes in nutrition, climate, and disease; see Garn et al. [1965] and references therein) that impact the development of other bodily systems. In the present analysis, the dental stage of each tooth for each individual was scored, and the midpoint of the age range for each individual was then transformed to a single year. All individuals (beyond the neonatal stage) in the sample are associated with dental elements with the exception of

the Krapina C3 partial cranium. Krapina C3 is recognized as an adult due to its size and degree of cranial suture closure (Radović et al., 1988).

Known ages for the comparative samples were included when available. A total of fifty-eight modern human infants and juveniles located at the Anatomie Museum, Rijksuniversiteit Leiden and the Anatomisch Museum, Rijksuniversiteit Groningen had assigned ages, although whether age was estimated at accession or whether it was determined from recorded age at death was uncertain since these historic collections were assembled between the seventeenth and nineteenth centuries (G. Maat and J. Le Grand, personal communication). A single modern human adult from the Centrum voor Fysische Antropologie, Rijksuniversiteit Leiden and seventeen humans from the Vakgroep Anatomie en Embryologie, Rijksuniversiteit Groningen (Utrecht series) had ascribed ages as did two juvenile *Pan* specimens from the Muséum National d'Histoire Naturelle. For the other individuals a variety of standard osteological methods were included to estimate age, such as patterns of dental eruption, neurocranial, facial and tympanic bone development, ossification of cranial sutures, palatal and sphenoid-occipital synchondroses, dental attrition and epiphyseal plate closure of the long bones when available.

Aging Neandertals and Modern Humans

Modern human developmental patterns were also employed in aging the Neandertal sample, although there is some evidence that Neandertals may have shown a more rapid (Stringer et al., 1990) or slightly later (Smith, 1991) eruption of M1 than that of modern *Homo sapiens*. The pace of dental development in Neandertals is currently hotly debated (cf. Ramirez Rozzi and Bermúdez de Castro, 2004; Macchiarelli et al., 2006; Smith et al., 2007, 2009; Guatelli-Steinberg and Reid, 2008; Bayle et al., 2009; Guatelli-Steinberg, 2009). In anthropoid primates, there is a very strong relationship between age at M1 eruption and adult brain mass (Smith, 1989), and between adult brain and body mass (Smith, 1991). Brain mass of Neandertal adults is found within the range of modern human variation (Trinkaus and Tompkins, 1990). Assuming brain size closely predicts M1 eruption in anthropoid primates, it is possible that the timing of M1 eruption in Neandertals did not widely depart from that of modern humans. Of course it is also possible that Neandertals differed from this expectation by maturing more rapidly than M1 eruption would predict. However, rates of enamel accumulation for Neandertals are at the lower edge but still within the range of variation sampled for modern humans (Dean, 2006).

Radiographs were accessible for several Neandertal juveniles (Skinner and Sperber, 1982; Legoux, 1966), but they were not available for all specimens examined, nor for the large modern human sample. For consistency, all individuals were aged without radiographs. Dental eruption scores were obtained for each deciduous (d) and permanent (P) tooth as follows: d_0/P_0 = no crypt present; d_1/P_1 = crypt present and crown calcified; d_2/P_2 = tooth at or near alveolar margin; d_3/P_3 = tooth one-third erupted; d_4/P_4 = tooth two-thirds erupted; d_5/P_5 = attainment of occlusal level. For Neandertals, estimated dental ages were broadly similar to those calculated by Minugh-Purvis (1988), who included calcification scores to estimate age in Upper Pleistocene and recent *Homo*.

To model growth, an estimated age in years had to be identified for each individual. For 182 modern human and 21 Neandertal non-adults, modern human dental aging charts were consulted to assign ages to the nearest half-year (Ubelaker, 1978; Buikstra and Ubelaker, 1994). Ages for 112 modern human and 21 Neandertal dental adults were estimated on the basis of basilar, palatal, and cranial suture ossification combined with the degree of tooth wear (Maat, 1987; Richards and Miller, 1991). A scoring system was developed for adults that included five stages. All dental adults were matched and seriated

as closely as possible to these criteria: 18–25 years = all teeth at occlusal plane, basilar suture scar visible, teeth unworn; 26–32 years = basilar suture closed, palatal and cranial sutures open, mild wear on teeth; 33–40 years = most palatal sutures closed, coronal and sagittal sutures in process of closing endocranially; 41–49 years = coronal and sagittal sutures in process of closing ectocranially, substantial tooth wear present; over 50 years = coronal suture closed, heavy tooth wear present. These criteria do not age the Neandertal adults very precisely. Specifically, dental attrition is extreme even in young Neandertal adults (e.g., La Ferrassie 1). For this reason, cranial suture closure and other osteological indicators were weighed more heavily than dental wear when assessing age in Neandertal adults.

Aging Pan

The dental aging score system (d_0 to d_5 for deciduous teeth, and P_0 to P_5 for permanent dentition) incorporated for Neandertals and modern humans was also employed for chimpanzees and bonobos. *Pan* specimens with all permanent teeth erupted were matched and seriated as closely as possible to the following criteria: 11–13 years = all teeth at occlusal plane, basilar and palatal sutures open (or scar visible), cranial sutures in process of closing, teeth unworn; 14–17 years = basilar suture closed (Poe, 2011), coronal and sagittal sutures closed, palatal sutures in process of closing, mild wear on teeth; 18–21 years = palatal sutures closed, substantial wear on anterior teeth, M1 and M2; 22–25 years = heavy tooth wear on all dental elements present; over 26 years = anterior dentition worn through to root, extensive wear on posterior dentition present, and alveolar resorption apparent.

Dental eruption schedules devised by Dean and Wood (1981) based partly on Nissen and Riesen (1964) for wild-caught *P. troglodytes* were employed to age both species of *Pan*. The dental eruption schedules for *P. troglodytes* were used to age immature *P. paniscus* for two reasons. First, all ape species appear to exhibit similar dental eruption patterns (Dean and Wood, 1981; Winkler et al., 1996). Second, precise standards for *P. paniscus* are unavailable in the literature (Smith et al., 1994). Because the dental developmental sequence of the individuals examined more closely corresponds to that observed by Dean and Wood (1981) than to those noted by other authors (e.g., Anemone et al., 1996; Kuykendall and Conroy, 1996), the Dean and Wood (1981) aging schedule was utilized. Schultz's (1933) deciduous dental aging chart for *P. troglodytes* was adopted for all very young chimpanzees and bonobos (birth to 1.3 years). Although the exact ages of these individuals are unknown, it is assumed that dental maturation schedules closely correspond to chronological age as reported among wild chimpanzees (Zihlmann et al., 2004).

Capturing Linear Dimensions

Twenty craniofacial measurements were utilized in this study to represent the Neandertal remains and to include the greatest number of individuals. The measurement definitions derived from Bass (1987) and Buikstra and Ubelaker (1994), except for mandibular length, which was developed to accommodate fragmentary fossil Neandertal mandibles. Measurements were taken from the left side unless damage to the individual necessitated using the right side. Permission to utilize a 3D digitizer was not obtained from all of the museums housing the most complete Neandertal remains. Many museum curators do not permit researchers to utilize modeling clay to precariously stabilize unique and fragmentary fossils for digitization purposes (Krovitz, 2000). To include as many fossils as possible, all dimensions were recorded using digital sliding calipers.

Eight measurements on the calvarium were taken and include maximum cranial length (glabella-opisthocranion), maximum cranial breadth (bi-parietal), minimum frontal breadth (maximum postorbital constriction), biorbital breadth (across the most lateral extremes of the fronto-maxillary suture), orbital breadth (maxillofrontale to ectoconchion), interbiorbital (bi-ectoconchion), upper cranial height (porion-bregma), and cranial base height (porion-basion). Measurements for the face were limited because of the poor preservation of the splanchnocranium in most Neandertals, but comprised biectomolare breadth (breadth across the most lateral extremes of the maxillary alveolus), palatal length (prosthion-staphylion), palatal breadth (bi-endomolare at widest point), maximum nasal aperture breadth (bi-alare), and upper facial height (alveolare-nasion). The relatively numerous Neandertal mandibles preferentially include the alveolus, much of the corpus, and the mental region. Often the mandibular and coronoid condyles are missing. Furthermore, the posterior border of the ramus and the inferior border of the body are often eroded or abraded in the fossils. The general dimensions of the fossil mandibles (and those from the comparators) were represented by seven measurements, including bigonial breadth, mandibular length (gonion-gnathion), mandibular symphysis height (infradentale-gnathion), mandibular corpus height (at the mental foramen), mandibular corpus thickness (at the mental foramen), ascending ramus height (gonion to the most superior aspect of the mandibular condyle), and maximum ascending ramus breadth (distance between the most anterior edge of ascending ramus and the most posterior aspect of the mandibular condyle).

Craniofacial Variability within the Modern Human Sample

To evaluate inter- and intrapopulation variation in craniofacial growth, the two most unique populations with available series of nonadults and adults, Papua New Guinea ($n = 24$) and Medieval Belgium ($n = 54$), were compared to a geographically varied sample of modern humans ($n = 216$). Both Papua New Guinea and Medieval Belgium trajectories could be easily accommodated with the variability characterizing the geographically varied ontogenetic sample. Additionally, the variation among population only slightly exceeds the variation within-population for the geographically varied ontogenetic sample. An ANOVA showed a lack of significant differences for sixteen out of twenty craniofacial dimensions when adults of Medieval Belgian, Papuan, and the geographically varied group are compared. T-tests between adults of the two most divergent populations, Medieval Belgium and Papua New Guinea, yield non-significant p values for seventeen out of twenty dimensions.

Modeling Growth

Each craniofacial ontogenetic trajectory for modern humans, Neandertals and the two species of *Pan* was interpolated using Piecewise Regression. This modeling technique is one of many regression procedures useful in generalizing cross-sectional data (de Bruin, 1993). Piecewise regression includes one part that demonstrates increasing growth and another that models the cessation and thus maturation of growth. These two parts are separated by an asymptotic value which demarcates the point at which the increase of a dimension terminates. The flat line behavior of the regression following the asymptotic value distinguishes piecewise regression from other interpolation methods such as von Bertalanffy's, Gompertz's, negative exponent, and simple power curves. Piecewise regression is a second order polynomial and therefore requires fewer assumptions concerning the nature of growth in contrast to other models which feature higher order polynomials (Williams et al., 2003; Williams and Krovitz, 2004). Furthermore, piecewise regression can generalize samples with relatively small numbers of individuals and thus is useful in characterizing fossil populations.

Piecewise Regression

Using the non-linear function in Systat 10.2, coefficients approximating rates and durations of growth were calculated from piecewise regression. From a maximum of fifty iterations using twenty half-steps of Gauss-Newton least squares, four coefficients were estimated for each of the twenty craniofacial dimensions. Starting values for the four coefficients allowed for initial estimates to identify global versus local minima, and therefore the best fit of the model to the data. The four beta (b) coefficients approximated the y-intercept, or size at birth (b_0), the initial growth rate (b_1), the decline in the growth rate (b_2), and the age at which growth levels for a given dimension (b_3), respectively (Leigh and Terranova, 1998). Piecewise regression produces a growth curve that flattens at the cessation of growth, such that

$$\text{Dimension} = \left((b_0 + b_1 * \text{age} + b_2 * \text{age}^2) * (\text{age} < b_3) + (b_0 + b_1 * b_3 + b_2 * b_3^2) * (\text{age} \geq b_3) \right)$$

The likelihood surface modeled to interpolate these ontogenetic series was constrained by imposing minimum and maximum values for each of the four coefficients. The y-intercept (b_0) was required to be between 1000 and -1000 ; the initial growth rate (b_1) was constrained to be positive (between 0 and 1000); the change in the rate of growth (b_2) was required to be no greater than -0.1 , except for all mandibular variables, and palatal and nasal breadths, which were restricted to be no greater than 0; b_3 was constrained to be between 0 and 25 years for *Homo* and between 1 and 14 for *Pan*. These constraints correspond to life history features, experimental evidence, and theoretical predictions of non-human and human growth (Hauspie, 1989; de Bruin, 1993; Leigh and Terranova, 1998). The modeled coefficients were then compared across taxa to approximate patterns of growth for Neandertals compared to modern humans and between the two species of *Pan*.

Multivariate Analyses

Modeled growth trajectories (see Figure 7.2 for an example) were subject to multivariate comparisons to show regional patterns of growth and shape change in the calvarium, face, and mandible, explored in separate principal components analyses. For all three regions the growth curves from piecewise regression are shown with the original data to demonstrate the relative variability around the models. To investigate differences in shape, each measurement was divided by the geometric mean of all dimensions comprising a particular region (calvarium, face, and mandible) before principal components analysis was conducted.

Euclidean Distances between Adults and Infants on Principal Components Axes

In order to examine whether the differences in postnatal ontogeny between Neandertals and modern humans exceed those found between the two species of *Pan*, Euclidean distances were calculated for modeled values for each taxon along principal components (PC) axes, conducted separately for the calvarium, the face, and the mandible. Differences between modeled adults and modeled infants (aged at 0.5 years) were calculated using the following equation, here shown for Neandertal adult-infant Euclidean distance:

$$\text{Distance} = \sqrt{(((\text{NadtPC1} - \text{NinfPC1}) * (\text{PC1v}))^2) + (((\text{NadtPC2} - \text{NinfPC2}) * (\text{PC2v}))^2)},$$

where NadtPC1 = Neandertal modeled adult value on PC axis 1; NinfPC1 = Neandertal modeled infant value on PC axis 1; PC1v = PC axis 1 variance explained; NadtPC2 =

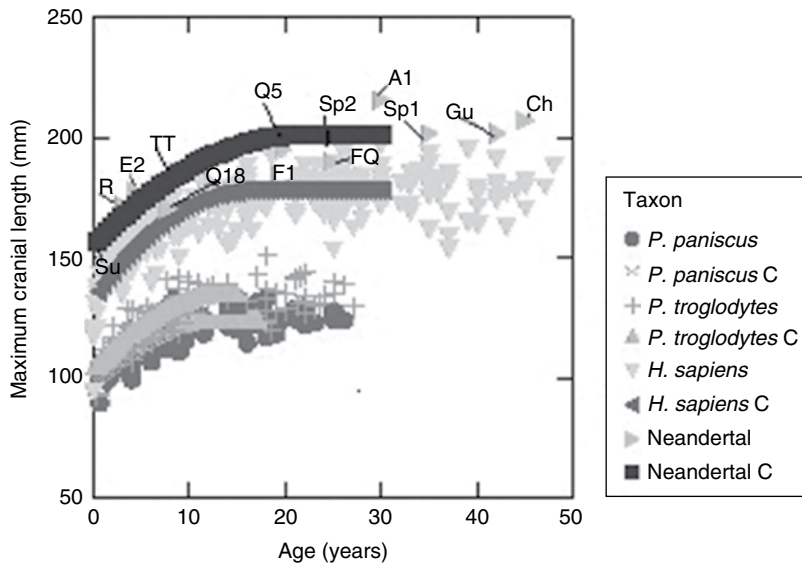


Figure 7.2. Maximum cranial length is well preserved in Neandertals and therefore provides an important way to estimate the growth of the cranial vault during postnatal ontogeny. Growth curves for the four taxa show that the lengthening of the cranium occurs rapidly after birth and that adult sizes are reached well before somatic maturation is complete. Neandertals include Subalyuk 1 (Su); Roc de Marsal (R); Engis 2 (E2); La Quina 18 (Q18); Teshik-Tash 1 (TT); La Quina 5 (Q5); La Ferrassie 1 (F1); Spy 2 (Sp2); Spy 1 (Sp1); Forbes' Quarry (FQ); Amud 1 (A1), Guattari (Gu); La Chapelle-aux-Saints (Ch).

Neandertal modeled adult value on PC axis 2; NinfPC2 = Neandertal modeled infant value on PC axis 2; and PC2v = PC axis 2 variance explained.

Results

Neandertal and Modern Human Modeled Growth Trajectories

For most craniofacial dimensions, Neandertals at birth (b_0), are larger than their modern human counterparts (Table 7.2). This larger size may derive from faster prenatal growth patterns in Neandertals (Green and Smith, 1990), despite a similar neonatal endocranial volume compared to those of modern humans (Ponce de León et al., 2008; Gunz et al., 2010). Modern humans, however, are larger at birth than Neandertals in orbital and palatal breadths, mandibular symphysis and corpus heights, and ascending ramus height and maximum breadth. Modern human neonates exhibit broader orbits and palates, a pronounced mental trigone and a taller mandibular symphysis and corpus compared to Neandertal young infants.

For maximum cranial length and breadth, upper cranial height, and cranial base height, a faster initial rate of growth (b_1) is exhibited by modern humans, perhaps reflecting a more globular neurocranial vault. The globular vault of modern humans occurs either during (Gunz et al., 2010) or after (Williams, 2001) the deciduous teeth are fully erupted. A relatively accelerated broadening of the mandibular corpus is also shown in modern humans (Table 7.2). Although Neandertals exhibit a thicker mandibular corpus at birth, modern humans eventually approximate Neandertals in mandibular corpus thickness through a faster initial growth rate.

Table 7.2. Modern human and Neandertal modeled growth parameters.

Craniofacial Dimensions	Modern Human Coefficients			Neandertal Coefficients				
	b0	b1	b2	b3	b0	b1	b2	b3
Maximum Cranial Length	133.1	5.83	-0.19	15.25	154.3	4.32	-0.10	21.59
Maximum Cranial Breadth	111.1	4.27	-0.18	12.13	119.0	3.39	-0.10	16.92
Minimum Frontal Breadth	71.63	3.08	-0.10	15.39	82.86	3.10	-0.10	15.50
Biorbital Breadth	69.59	3.58	-0.10	17.91	77.05	4.09	-0.10	20.46
Orbital Breadth	24.27	1.73	-0.08	10.81	22.31	2.72	-0.10	13.59
Interbiorbital Breadth	64.24	3.34	-0.10	16.70	70.83	3.69	-0.10	18.44
Upper Cranial Height	87.31	6.50	-0.29	11.37	99.55	3.21	-0.10	16.02
Cranial Base Height	33.49	3.30	-0.10	16.48	42.75	3.27	-0.10	16.33
Biectomolare Breadth	38.11	3.04	-0.10	15.21	39.65	3.50	-0.10	17.50
Palatal Length	21.54	3.23	-0.10	16.14	22.67	3.55	-0.11	15.69
Nasal Breadth	13.32	1.10	-0.03	18.33	15.53	1.47	-0.03	24.47
Upper Facial Height	34.98	3.65	-0.10	18.26	43.83	3.94	-0.10	19.59
Palatal Breadth	20.25	1.36	-0.03	22.70	18.47	2.56	-0.06	21.33
Bigonial Breadth	54.18	2.98	-0.05	21.00	59.78	2.65	-0.05	25.00
Mandibular Length	43.23	3.51	-0.07	23.75	44.53	4.00	-0.08	25.00
Symphysis Height	15.85	1.20	-0.02	21.00	14.47	1.62	-0.03	25.00
Corpus Height	12.77	1.38	-0.03	22.00	12.55	1.49	-0.03	24.76
Corpus Breadth	9.04	0.26	-0.006	19.46	10.48	0.66	-0.02	14.76
Ramus Height	22.37	3.03	-0.06	23.90	21.37	3.95	-0.01	19.76
Maximum Ramus Breadth	21.08	1.93	-0.04	22.14	20.88	1.85	-0.03	21.92

Neandertals and modern humans are broadly similar in the decline in the rate of growth (*b2*), although following a faster initial growth rate, modern humans mature earlier in the growth of maximum cranial length and breadth, and upper cranial height. For the breadth of the mandibular corpus, Neandertals exhibit a much slower decline in the rate of growth when compared to modern humans.

In Neandertals, several craniofacial dimensions continue growth for an extended duration (*b3*) relative to modern humans. An exception is the cranial base which in modern humans continues growth for longer than it does in Neandertals. This extension may indicate continued growth of the flexed cranial base in modern humans (Laitman and Heimbuch, 1982). Modern humans also exhibit a later maturation of palatal dimensions (Table 7.2). In contrast, Neandertals are characterized by a more rapid growth of palatal length and breadth but within a shorter time frame perhaps corresponding to an accelerated calcification and eruption of the second and third molars (Wolpoff, 1979; Tomkins, 1996). The height and maximum breadth of the mandibular ascending ramus exhibits a longer growth period in modern humans when compared to Neandertals. Neandertals, however, show a faster initial rate of growth of the ascending ramus eventually leading to larger adult values than is the case for modern humans.

Modeled Growth Trajectories for the Two Species of Pan

Pan paniscus is generally smaller than *P. troglodytes* in the sizes of modeled craniofacial dimensions at birth (*b0*) (Table 7.3). It has long been recognized that *P. paniscus* exhibits a taller and broader cranium coupled with a reduced amount of postorbital constriction when compared to *P. troglodytes* (Coolidge, 1933). Accelerated initial growth rates (*b1*) for maximum cranial breadth, minimum frontal breadth, and upper cranial height in *P. paniscus* may result in these distinctions (Table 7.3). A more rapid rate of facial height growth is exhibited by *P. paniscus*. By adulthood, however, the face is taller in *P. troglodytes* from a larger size at birth (*b0*) and a longer duration of growth (*b3*) compared to *P. paniscus*. Adults of *P. troglodytes* achieve greater prognathism and postorbital constriction, as well as a larger overall craniofacial region than do *P. paniscus* adults by growing for a longer duration for most dimensions with the exception of palatal length and ascending ramus height (Table 7.3).

Multivariate Analyses of the Calvarium

For the calvarium, both PC axes show an ontogenetic signal for all taxa, although it is much stronger along the second PC axis. The first axis distinguishes the two genera, *Homo* and *Pan*. Modern human juveniles are similar in size to Neandertal infants and modern human adults are smaller than Neandertal late subadults and adults in calvarium size. La Chapelle-aux-Saints and La Ferrassie 1 stand out as distinctly larger in calvarium size than Guattari 1 and the largest of the modern human adults. The two species of *Pan* follow similar calvarium growth trajectories, although *P. paniscus* is smaller at birth and diverges from *P. troglodytes* during subadulthood. Modern humans exhibit a remarkably short postnatal ontogenetic trajectory of the neurocranium compared to the Neandertals and *Pan* (Figure 7.3a). The first axis is largely capturing size differences reflected in the highly positive component loadings for PC axis 1. The second axis separates infants of all taxa with proportionally large cranial vaults, from adults with relatively large orbital and cranial base dimensions vis-à-vis the neurocranium (Table 7.4). Some Neandertal adults, such as La

Table 7.3. *Pan paniscus* and *P. troglodytes* modeled growth parameters.

Craniofacial Dimensions	P. paniscus Coefficients			P. troglodytes Coefficients				
	b0	b1	b2	b3	b0	b1	b2	b3
Maximum Cranial Length	97.54	3.93	-0.15	13.73	103.2	4.36	-0.15	12.07
Maximum Cranial Breadth	82.80	3.28	-0.25	6.69	85.74	3.22	-0.21	7.77
Minimum Frontal Breadth	55.14	3.17	-0.23	6.14	61.92	2.40	-0.17	7.30
Biorbital Breadth	50.52	5.59	-0.20	13.97	56.67	6.17	-0.20	14.00
Orbital Breadth	20.03	2.07	-0.10	10.33	21.18	2.16	-0.10	10.81
Interbiorbital Breadth	46.86	3.87	-0.12	13.47	48.50	5.40	-0.20	13.49
Upper Cranial Height	67.58	2.47	-0.12	9.95	72.98	2.18	-0.10	10.89
Cranial Base Height	31.34	3.55	-0.13	13.46	36.26	3.65	-0.14	11.88
Biectomolare Breadth	34.01	2.71	-0.10	14.00	34.81	3.92	-0.15	13.05
Palatal Length	24.10	4.59	-0.15	14.00	24.61	6.90	-0.25	14.00
Nasal Breadth	9.86	1.34	-0.05	13.35	10.46	1.97	-0.07	13.98
Upper Facial Height	36.87	5.77	-0.21	13.74	44.46	5.46	-0.15	14.00
Palatal Breadth	13.46	2.29	-0.10	11.43	15.80	2.55	-0.10	12.73
Bigonial Breadth	37.34	3.97	-0.13	13.78	42.70	5.40	-0.17	14.00
Mandibular Length	32.23	5.12	-0.15	12.70	40.33	6.47	-0.20	13.90
Symphysis Height	16.67	1.86	-0.05	13.98	17.87	3.06	-0.10	14.00
Corpus Height	12.60	1.49	-0.05	13.80	13.16	2.58	-0.10	12.89
Corpus Breadth	7.58	0.67	-0.03	12.45	6.66	1.74	-0.10	8.70
Ramus Height	21.12	3.56	-0.10	14.00	20.00	5.60	-0.20	14.00
Maximum Ramus Breadth	15.56	2.87	-0.07	13.55	14.70	5.33	-0.20	14.00

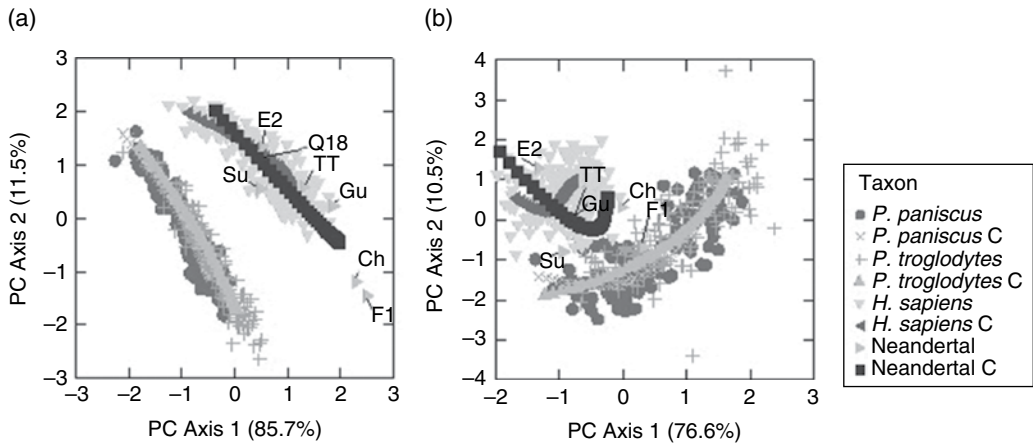


Figure 7.3. Principal components analysis of calvarium dimensions showing unscaled (a) and scaled (b) comparisons of raw data and modeled growth curves (C) for each taxon. Neandertals include Engis 2 (E2); Subalyuk 2 (Su); La Quina 18 (Q18); Teshik-Tash 1 (TT); Guattari (Gu); La Chapelle-aux-Saints (Ch); La Ferrassie 1 (F1).

Chapelle-aux-Saints and La Ferrassie, exhibit excessively large orbital regions and are projected as highly negative on PC axis 2.

When calvarium dimensions are scaled to the geometric mean, the first PC axis distinguishes infants from adults, whereas the second one better separates taxa (Figure 7.3b). The first axis also separates modern humans of all ages on the basis of their relatively large cranial vaults from adult *Pan* with relatively large orbital superstructures (Table 7.4). The two species of *Pan* are much more similar to one another on both axes than are Neandertals and modern humans. La Ferrassie 1 is distinct from the other Neandertal adults in exceeding the variation in modern humans, whereas Subalyuk 2 is close to the extremes of human variation. The other Neandertals, including Engis 2, Teshik-Tash 1, and Guattari 1, all fall within the range of modern humans at various life cycle stages. Nevertheless, the modeled growth curves with respect to size are distinct in form and length between Neandertals and modern humans. And although modern human subadults share some aspects of calvarium shape with infant Neandertals, modeled Neandertal adults fall outside the distribution of observed modern human adults.

Multivariate Analysis of Facial Dimensions

For unscaled facial dimensions (or size-shape space), PC axis 1 exhibits a strong ontogenetic signal while the second PC axis distinguishes *Pan* and *Homo* on the basis of an elongated upper face and palate in the former (Figure 7.4a; Table 7.4). Both modern humans and *P. paniscus* are typified by shorter growth trajectories compared to those of Neandertals and *P. troglodytes*, respectively. Amud 1 and Tabūn C1 exhibit large facial regions and particularly wide alveolar processes (Table 7.4), compared to modern humans, whereas Guattari 1 approximates the largest modern human adult specimens. Modern human adults are similar in facial size to Neandertal infants, and *P. paniscus* subadults resemble *P. troglodytes* juveniles in facial size. Modern humans exhibit a rather short postnatal ontogenetic trajectory for the face compared to the other taxa.

Table 7.4. PCA component loadings for size-shape space (unscaled) and shape space (each dimension scaled by dividing by the geometric mean).

Dimensions	Size-Shape Space		Shape Space	
	PC Axis 1	PC Axis 2	PC Axis 1	PC Axis 2
Maximum Cranial Length	0.959	0.244	-0.837	0.402
Maximum Cranial Breadth	0.909	0.394	-0.920	-0.185
Minimum Frontal Breadth	0.946	0.284	-0.861	-0.262
Biorbital Breadth	0.913	-0.378	0.943	0.225
Orbital Breadth	0.927	-0.300	0.797	-0.476
Interbiorbital Breadth	0.974	-0.185	0.817	0.494
Upper Cranial Height	0.915	0.371	-0.918	0.189
Cranial Base Height	0.856	-0.463	0.900	-0.136
Biectomolare Breadth	0.947	0.251	0.659	-0.732
Palatal Length	0.725	-0.661	-0.933	0.051
Nasal Breadth	0.852	0.319	0.813	0.455
Upper Facial Height	0.852	-0.469	-0.888	-0.104
Palatal Breadth	0.902	0.387	0.888	0.078
Bigonial Breadth	0.876	0.426	0.642	-0.653
Mandibular Length	0.980	0.102	0.743	-0.086
Symphysis Height	0.884	-0.373	-0.828	0.393
Corpus Height	0.964	0.069	0.004	0.345
Corpus Breadth	0.838	-0.364	-0.563	-0.749
Ramus Height	0.950	0.167	0.525	0.586
Maximum Ramus Breadth	0.964	-0.067	0.134	0.589

When multivariate facial dimensions are scaled, by dividing each measurement by the geometric mean, there is a nearly complete distinction between *Pan* and *Homo* on the first axis. The first PC axis separates *Pan*—on the basis of their elongated upper faces and palates with respect to size—from *Homo* with relatively wide nasal apertures and alveolar processes (Figure 7.4b; Table 7.4). The second axis polarizes infants from adults on the basis of the relative proportions of the maxilla (Figure 7.4b; Table 7.4). *Pan paniscus* subadults are similar in facial shape to juvenile *P. troglodytes*. Modern humans exhibit a particularly short facial shape change trajectory along the second axis. Neandertals and modern humans do not exhibit overlap in scaled modeled growth parameters, although modern human adults more closely resemble modeled Neandertal juveniles than any other Neandertal life cycle stage. Infant Pech de l’Azé resembles modern human late subadults in modeled facial shape and La Quina 18 also falls within the range of modern humans. Roc de Marsal and Teshik-Tash 1 nearly fall within the range of modern human facial shape, but Amud 1 and particularly Guattari 1 and Tabūn C1 exhibit extreme positive values when compared to the distribution of modern human adults (Figure 7.4b).

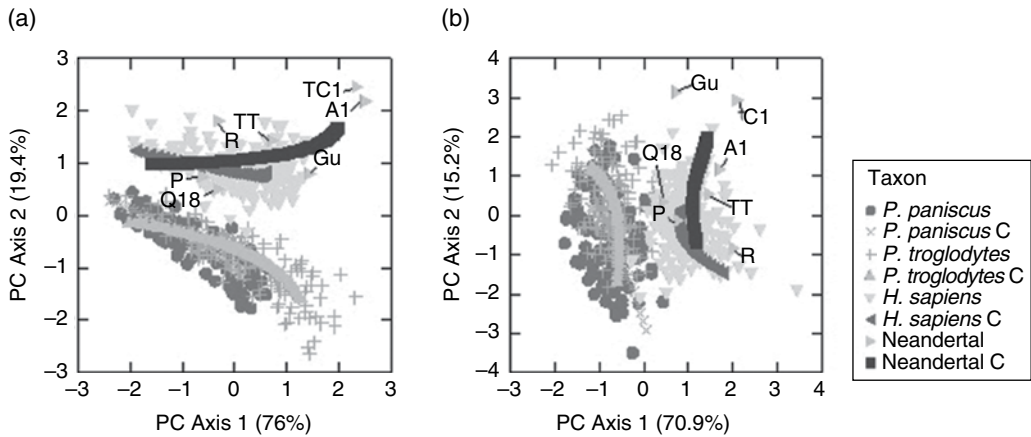


Figure 7.4. Principal components analysis of facial dimensions showing unscaled (a) and scaled (b) comparisons of raw data and modeled growth curves (C) for each taxon. Neandertals include Pech de L'Azé (P); Roc de Marsal (R); La Quina 18 (Q18); Teshik-Tash 1 (TT); Guattari (Gu); Tabün C1 (TC1); Amud 1 (A1).

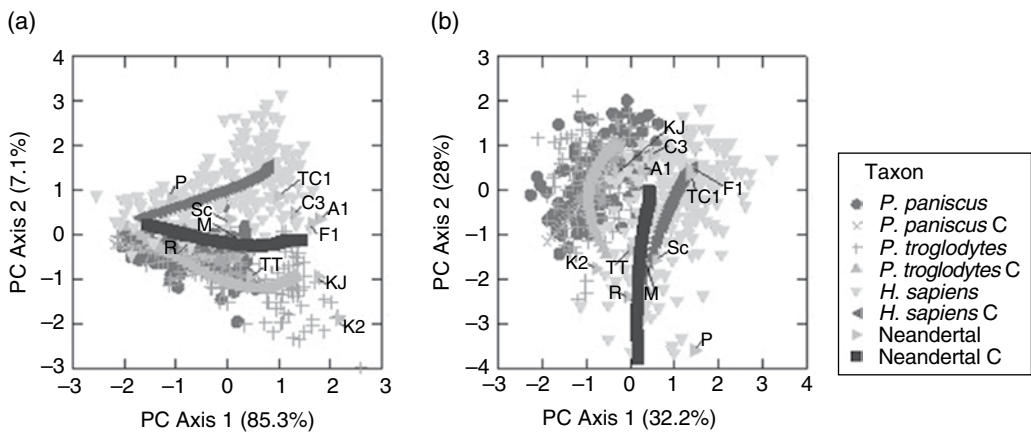


Figure 7.5. Principal components analysis of mandibular dimensions showing unscaled (a) and scaled (b) comparisons of raw data and modeled growth curves (C) for each taxon. Neandertals include Pech de L'Azé (P); Roc de Marsal (R); Scalyn (Sc); Malarnaud (M); Teshik-Tash 1 (TT); Tabün C1 (TC1); Monte Circeo 3 (C3); Amud 1 (A1); La Ferrassie 1 (F1); Krapina Mandible J (KJ); Kebara 2 (K2).

Multivariate Analysis of Mandibular Dimensions

The first PC axis for unscaled mandible dimensions (or size-shape space) exhibits a strong ontogenetic trajectory, whereas the second PC axis distinguishes taxa on the basis of the relatively broad bigonial breadths in *Homo* and the relatively expanded symphyses and corpora in *Pan*, Krapina Mandible J, and Kebara 2 (Figure 7.5a; Table 7.4). Neandertals and modern humans do not differ substantially in trajectory lengths along PC axis 1, which primarily describes increasing mandibular size from infancy to adulthood. Most Neandertal adults exhibit mandibular sizes within the distribution of modern humans, including Amud 1, Circeo 3, La Ferrassie 1, and Tabün C1. Along PC axis 2, modern humans and

Neandertals are distinct with no overlap of modeled growth curves. Krapina Mandible J, Kebara 2, and, to a lesser extent, Teshik-Tash 1 exhibit relatively ape-like mandibles, whereas Amud 1, Circeo 3, La Ferrassie 1, Tabün C1, Sclayn, and Roc de Marsal are more similar to modern humans on the second PC axis.

When mandibular dimensions are scaled by dividing each by the geometric mean, the first PC axis separates *Homo* and *Pan*. The second axis separates infants from adults, projected from a negative to positive direction, respectively (Figure 7.5a). Krapina Mandible J and Kebara 2 exhibit the most ape-like mandibles primarily on the basis of their tall mental symphyses and thick mandibular corpora (Table 7.4), whereas those attributed to La Ferrassie 1 and Tabün C1 are more human-like; Circeo 3 and Amud 1 fall between these two extremes. La Ferrassie 1 and Tabün C1 fall along the human modeled growth curve scaled to the geometric mean. Similarly, Sclayn resembles some aspects of infant human modeled mandibular shape. Roc de Marsal and particularly Pech de l'Azé are distinct in mandibular shape compared to modern human infants along the second PC axis. Modern human infants most resemble Neandertal juveniles in modeled mandibular growth scaled to the geometric mean. When the effects of size are controlled for, Neandertals exhibit a relatively elongated growth trajectory on PC axis 2, implying profound postnatal mandibular shape changes occurred during maturation (Figure 7.5b).

Euclidean Distances between Adults and Infants

Figure 7.6 shows the relative differences for each craniofacial region per taxon. Differences between adults and infants in growth and shape change of the calvarium along PC axes 1 and 2 in Figure 7.3a suggest that ontogenetic size distinctions between Neandertals and modern humans exceed those found between the two species of *Pan*. When calvarium dimensions are divided by the geometric mean (Figure 7.3b), the two species of *Pan* exhibit similar amounts of calvarium infant to adult transformation, whereas Neandertals change over twice as much as do modern humans during postnatal ontogeny (Table 7.5). When the face is considered, the combined size and shape differences are greatest for Neandertal postnatal ontogeny, and the differences between Neandertals and modern humans exceed that found between the two species of *Pan* (Figure 7.4a). However, when facial dimensions are scaled, the greatest difference in postnatal ontogeny is present between *P. paniscus* and *P. troglodytes* (Figure 7.4b). In all comparisons of the mandible, including those for which size is controlled for, the ontogenetic differences between *P. troglodytes* and *P. paniscus* exceed those observed between Neandertals and modern humans (Figure 7.5).

Discussion

Neandertal postcranial ontogeny remains an important topic of investigation in paleoanthropology because the volume of individuals represented at different developmental ages can address questions related to the evolution of human life history, heterochrony, the modern human origins debate, craniofacial growth, dental development, paleopathology, and paleodemography. However, the sample available to examine Neandertal postnatal ontogeny is temporally and spatially broad, and some individual may not be as closely related to the others. For example, Glantz et al. (2009) found that juvenile Teshik-Tash 1 only poorly approximates the craniofacial form characterizing Neandertal non-adults from Western Europe. If true it suggests that Neandertals may have not extended as far to the east (Uzbekistan) as previously thought. However, the well-preserved Neandertal juveniles Glantz et al. (2009) included (namely La Quina 18) are substantially younger than is

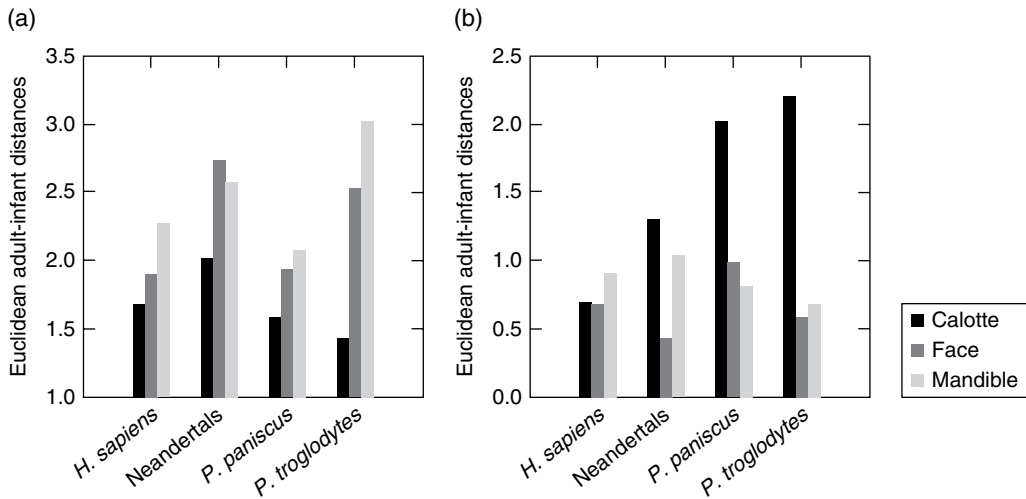


Figure 7.6. Euclidean distances between modeled adults and modeled infants, using values from PC axes for unscaled (a) and scaled (b) analyses.

Table 7.5. Euclidean distances between adults and infants for each principal components analysis including size-shape space (unscaled) and shape space (each dimension scaled by dividing by the geometric mean).

Taxon	Calvarium		Face		Mandible	
	Size-Shape	Shape	Size-Shape	Shape	Size-Shape	Shape
<i>H. sapiens</i>	1.67	0.69	1.91	0.68	2.28	0.92
Neandertals	2.01	1.31	2.73	0.45	2.57	1.05
<i>P. paniscus</i>	1.59	2.04	1.94	0.99	2.08	0.82
<i>P. troglodytes</i>	1.46	2.21	2.52	0.60	3.02	0.67

Teshik-Tash 1. Therefore, modification of the cranium during late childhood/early sub-adulthood was not considered in estimating missing data using expectation-maximization and multiple imputation (Glantz et al., 2009). Glantz et al. (2009) maintain that constraining the sample to the available fossils, or “complete-sets,” is inferior to the imputation of missing data because the former is non-random. However, Neandertal juveniles are quite variable (Tillier, 1995), and it may be misleading to include estimates of missing data in multivariate analyses. Glantz et al. (2009) effectively test from the imputation of missing data whether Teshik-Tash 1 (9.5 years) approximates La Quina 18 (7.5 years), a relatively gracile cranium with only an incipient supraorbital torus and occiput compared to Teshik-Tash 1. Because La Quina 18 does not preserve the basal portion of the occipital squama, extending to the foramen magnum, along with parts of the occipital, parietal, and temporal bones on the right posteroinferior portion of the cranium, it could not be included in the comparison of the calvarium presented here. However, in the shape of the calvarium, Teshik-Tash 1 falls very close to Guattari 1 and secondarily to Subalyuk 2 (Figure 7.3b). In terms of facial shape Teshik-Tash 1 most closely approximates Amud 1, Roc de Marsal, and Pech de l’Azé and is similar to La Quina 18 on PC axis 2, which explains only 15.2% of the variation (Figure 7.4b). Since La Quina 18 does not preserve a mandible, it could not be compared to Teshik-Tash 1. However, for mandibular shape, Teshik-Tash 1 resembles Sclayn and

Malarnaud, and secondarily Kebara 2 (Figure 7.4b). Other authors have remarked on the affinity of Teshik-Tash 1 to Neandertals (Weidenreich, 1945; Minugh-Purvis, 1988; Tillier 1995). Contra Glantz et al. (2009), Teshik-Tash 1 falls within the anticipated range for a Neandertal late juvenile with respect to this sample ($n=41$) of Neandertals.

Reconstruction of Life History Parameters in Neandertals

Generally, Neandertals and *P. troglodytes* are larger than their modern human and *P. paniscus* counterparts throughout postnatal ontogeny. However, modern humans (and, to some extent, *P. paniscus*) have relatively taller cranial vaults from infancy onward. Most craniofacial dimensions in all four taxa continue growing into adulthood, although some dimensions of the calvarium terminate growth earlier than do most masticatory ones. Neandertal adults are extreme in the shape of the cranial vault compared to Neandertal children (Figure 7.1), suggesting substantial amplification of the craniofacial region occurred during subadulthood and early adulthood in Neandertals (Table 7.2).

Inferences from these observations are commensurate with investigations of Neandertal life history that suggest that the duration of maturation in Neandertals and modern humans are comparable (Trinkaus and LeMay, 1982; Minugh-Purvis, 1988; Smith, 1991; Tompkins, 1996; Dean et al., 2001; Dean, 2006; Macchiarelli et al., 2006; Williams, 2006; Guatelli-Steinberg and Reid, 2008; Ponce de León et al., 2008; Bayle et al., 2009; Guatelli-Steinberg, 2009), rather than Neandertals exhibiting an accelerated rate of maturation (Ramirez Rozzi and Bermúdez de Castro, 2004; Smith et al., 2007, 2009). The lack of significant differences in humeral and femoral bone strength between Neandertal and modern human children also suggests that the differences in adults arose late in postnatal development (Cowgill, 2010). Neandertal infant and juvenile postcrania are generally smaller than even the smallest-bodied modern humans (Cowgill, 2010), suggesting that the larger body sizes of adults occurred after M2 or even possibly M3 eruption. This reinforces the argument of a prolonged rather than a truncated duration of maturation in Neandertals. Furthermore, Neandertals and modern humans are similar in the position of the neonatal line in the developing dentition (Macchiarelli et al., 2006), and the large Neandertal neonatal cranial size, as reconstructed from the Mezmaiskaya infant, suggests that Neandertals and modern humans shared key life history traits in common (Ponce de León et al., 2008). Alternatively, Neandertal maturation may have been delayed with respect to that of modern humans (Ponce de León et al., 2008; see also Smith, 1991).

Differences in absolute rates and durations of craniofacial growth are apparent for the four taxa, at least as inferred from stages of dental maturation. Neandertals and *P. troglodytes* most often achieve greater sizes for craniofacial dimensions by growing at a faster rate and for a longer duration than is the case for modern humans and *P. paniscus*, respectively; this distinction is more marked in the Neandertal and modern human comparison than in *Pan.* However, for maximum cranial length and breadth dimensions, modern humans grow faster but for a shorter period of time than do Neandertals, and modern human palatal length grows at a slower rate, but for a longer duration, than in Neandertals, despite the relative late ossification of the premaxillary suture noted in Roc de Marsal and Engis 2 (Maureille and Bar, 1999). Neandertal adults achieve their expanded nasal apertures via a greatly extended duration of growth, as reconstructed from patterns of dental maturation, rather than by a faster rate of growth alone; much of this growth occurs during subadulthood, after M2 has erupted (Williams, 2006).

Overall, Neandertal life cycle stages can be distinguished from those of modern humans by their comparatively long and narrow crania, combined with broad brow regions and pronounced postorbital constriction. Additionally, Neandertal infants, with relatively truncated palates, and

adults, with expanded nasal regions can be separated from adult modern humans who exhibit comparatively elongated palates, and infant modern humans, who show relatively widened lower maxillae. Neandertal adults vary, but many individuals can be characterized as having relatively long mandibles with relatively tall mental regions. Neandertal infants have comparatively broad mandibles with reduced mental symphyses. Similar proportions are demonstrated when modern human adults are compared to their infants. Infant modern humans exhibit a thickened and short corpus of the mandible and, in this way, resemble Neandertals regardless of life cycle stage. Modern human adults in comparison exhibit relatively tall mandibular corpora and relatively wide gonial dimensions with respect to the other life cycle stages of either taxon.

Differences in postnatal ontogeny between modern humans and Neandertals can be evaluated against distinctions arising during growth and development in *Pan*. The comparison with *Pan* is an appropriate one, as *P. paniscus* and *P. troglodytes* have been compared in allometric and heterochronic frameworks. Specifically, *Pan paniscus* has been claimed to be neotenic with respect to the *P. troglodytes* (Shea, 1983a,b, but see Godfrey and Sutherland, 1995a,b, 1996). From the analysis presented here, *P. paniscus* adults can be distinguished from adult *P. troglodytes* by exhibiting a shorter cranial vault and a narrow orbital region. The infants of both *Pan* taxa can be characterized by wide lower maxillae while the adults exhibit elongated palates. However, the nasal aperture in *P. troglodytes* is considerably wider from infancy to adulthood with respect to *P. paniscus*. The mandibles of the two *Pan* taxa offer additional distinctions. In *P. troglodytes* infants, the mandible is relatively taller and thicker with more robust and taller mandibular corpora when compared to *P. paniscus* infant mandibles. With respect to the global ontogenetic differences exhibited between modern humans and Neandertals, those within *Pan* are generally less extreme when observed versus expected total craniofacial differences in shape are compared (Williams et al., 2003), but whether this is grounds for a species-level distinction between Neandertals and modern humans continues to generate debate (e.g., Harvati et al., 2004; Ackerman, 2005). When Euclidean distances between modeled adult and infant values along PC axes are compared for each taxon (Figure 7.6), the differences between the two species of *Pan* are exceeded by Neandertals and modern humans only for the calvarium and the size of the face. When facial dimensions are scaled, and for all mandible comparisons, postnatal ontogenetic differences exhibited between the two species of *Pan* are greater than those found between Neandertals and modern humans. In other words, grounds for a species-level distinction between Neandertals and modern humans, using the two species of *Pan* as a benchmark, is not supported when modeled growth curves are considered (Figure 7.6, Table 7.5). Schillaci et al. (2005) also suggest that Neandertals and modern humans are not separate species on the basis of macaque hybrid allometries.

Neandertal Postnatal Growth and the Emergence of Craniofacial Superstructures

In Neandertals, older infants and juveniles exhibit a relatively large calvarium and orbital region with respect to adults suggesting only minimal increases in these areas occurred after the eruption of the second molar. In contrast, the mandible in Neandertals is characterized by extensive growth from infancy to adulthood. Infant and juvenile Neandertals show similarities in cranial breadth, postorbital constriction, upper cranial height, length of the cranial vault, the palate, the supraorbital torus and dimensions of the cranial base suggesting that much of the growth in these regions occurred prior to the eruption of M1 rather than between the eruption of M1 and M2 (Williams, 2001). Older infants and juveniles depart in the height of the cranial vault indicating considerable growth occurred in this region prior to the eruption of M1, but then leveled off thereafter. Other Neandertal craniofacial dimensions increased substantially between the eruption of M2 and M3 including occipital and parietal bone lengths, cranial breadth, palatal length and various dimensions of the cranial base

(Williams, 2001). The mandibular corpus, swollen from the erupting dentition during the infant and the juvenile periods, remains robust throughout postnatal ontogeny.

Neandertals exhibited accelerated growth of the masticatory system, including the ascending ramus of the mandible and the upper face between infancy and adulthood. The palate lengthened considerably between the juvenile and adult life cycle stages to house the newly erupted posterior molars, perhaps corresponding to the maintenance of the premaxillary suture (Maureille and Bar, 1999). Length of the cranium and protrusion of the face continued to increase between infancy and maturation, and perhaps beyond the eruption of M3, reflected in the prognathic faces of adults and the prolongation of growth of the occiput into adulthood (Trinkaus and LeMay, 1982).

Neandertal adult, but not infant, mandibles often present pterygoid tuberosities located along the medial border of the gonial surface. These muscle markings commence formation around the time of the eruption of the second molar. For example, Teshik-Tash 1 does not have pterygoid tuberosities. In contrast, Sclayn and Krapina Mandible C do exhibit this feature (Williams, 2001). Some Neandertal mandibles are extreme in size and shape when compared to all extant taxa, such as Kebara 2 and Krapina Mandible J (Figure 7.5a). The supraorbital torus is rather gracile in infants such as Roc de Marsal and juveniles such as La Quina 18, when compared to adults such as Spy 1. In Teshik-Tash 1, the supraorbital region is more pronounced than in younger Neandertals but is not as enlarged and anteriorly expanded as it is in adults. The lack of preserved subadult Neandertal calvaria between the ages of 12 and 14 years limits the understanding of how and when this trait began to approach adult sizes. Nasal breadth is relatively small in Neandertal infants and juveniles and probably expanded greatly between the emergence of M2 and M3 but unfortunately the preservation of this region in subadults is severely limited. The occipital region is only slightly enlarged in infant and juvenile Neandertals (Figure 7.1) and probably increased substantially after the eruption of the second molar (Trinkaus and LeMay, 1982). The anterior mandible is quite variable, particularly among the Krapina Neandertals. Whereas some individuals exhibit a markedly short anterior mandible, others are relatively tall, perhaps signally differences between the sexes (Radović et al., 1988). For all of these traits, differences in initial postnatal sizes, as well as rates of growth and maturation times, are responsible for distinctions between Neandertal and modern human adults.

Conclusions

The growth of the calvarium, face and mandible differ substantially across taxa (Tables 7.2 and 7.3). But the major divisions are between *Pan* and *Homo* rather than within these genera. The differences in multivariate growth and shape change during postnatal ontogeny between Neandertal and modern human are smaller than differences between the two species of *Pan* for facial shape and for mandible dimensions, including those scaled to the geometric mean, but for the calvarium, Neandertals and modern humans differ more than do the two species of *Pan* (Figures 7.3–7.5). What these differences imply is that changes in the calvarium between infancy and adulthood are extreme between Neandertals and modern humans (Figure 7.6). Whether this difference is grounds for a species-level distinction between Neandertals and modern humans lacks support from modeled growth trajectories.

Neandertal Postnatal Ontogeny and Modern Human Origins

Inferring growth rates and maturation times for Neandertals provides fundamental insights about the evolution of modern human life history and, therefore, modern human origins,

particularly since large numbers of immature early modern human specimens are absent from the fossil record (Minugh-Purvis, 1988). Specifically, Neandertals can be utilized as a proxy for the growth and development of Middle Pleistocene *Homo* if indeed Neandertals retained the ontogenetic profile of the common ancestor, and there is every indication that indeed they did (Stringer et al., 1990). To the extent to which Neandertals do resemble Middle Pleistocene *Homo*, modern humans can be said to have modified ancestral ontogenetic trajectories by generally reducing rates of growth and consequently the size of the craniofacial skeleton (Ponce de León et al., 2008). The shape of the mandible and calvarium and, to a lesser extent, the facial skeleton, has also been modified (Holton and Franciscus, 2008), along with an elevation of the nasal floor (Franciscus, 2003) and a rounding of the suprainiac fossa region (Balzeau and Rougier, 2010). However, there is no uniform developmental signal from modeled growth curves that Neandertals matured earlier than their modern human counterparts. Modern humans have maintained, increased, and decreased the duration of craniofacial maturation depending on which dimension is examined. For example, the mandible and palate may have matured slightly earlier in Neandertals, but for the dimensions of the calvarium, Neandertals may have grown for a longer duration than is the case for modern humans. Neandertals are also not consistent in exhibiting faster rates of craniofacial growth. For example, cranial length and upper cranial height in modern humans grow faster, but for a shorter time interval, than in Neandertals. Although modern humans may have evolved at different rates and durations of craniofacial growth rather recently, the length of maturation, albeit costly, may have been only minimally modified since the evolution of large adult brain size in the Middle Pleistocene.

With respect to the origins of modern humans, the growth and developmental trajectories of Pleistocene relatives such as the Neandertals provide a valuable source of information regarding the evolution of modernity, particularly since it is ontogenies rather than adult morphologies that evolve (Zollikofer and Ponce de León, 2010). Although Neandertals are larger at birth compared to modern humans (Cartmill and Smith, 2009), the two are not uniformly more distinct from one another with respect to the differences apparent between the two species of *Pan*, suggesting perhaps that Neandertals and modern humans do not represent separate species. The recent African origin model is thus unsupported, as the evolution of recent humans may not have involved a speciation event (Stringer and Andrews, 1988). However, Neandertals and modern humans exhibit distinct ontogenetic signatures such that it cannot be said that the latter represents an extension of the shape path of the former (Williams et al., 2002). The variability of Neandertal infants and juveniles, as well as the observation that some Neandertals fall close to the idealized growth model for modern humans, suggests the Assimilation Model (Smith et al., 2005) may best account for distinctions in postnatal ontogeny characterizing Neandertals and modern humans.

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Note

1. The right femur and right humerus of La Ferrassie 4bis should be attributed to Le Moustier 2 according to Maureille (2002), removing La Ferrassie 4 as evidence of a Neandertal double burial.

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Chapter 8

Energetics and the Origin of Modern Humans

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... nothing in biology exists without energy flux.

Douglas C. Wallace, 2010

Bioenergetics is the study of energy exchange between organisms and their environments, and the allocation of energy to different functions within organisms. While living and non-living entities alike exchange energy with their surroundings, the acquisition and repurposing of environmental energy toward self-replication distinguishes living beings from other energy-bearing units, and provides the fundamental theoretical basis for bioenergetics research. Energy serves a variety of biological purposes, such as fueling metabolic processes, enabling physical activity, and facilitating tissue growth and maintenance, but its most important role, and one to which its other uses relate, is to fund reproduction. As reproductive success is the key to natural selection, the ability to direct energetic resources to reproduction is a fundamental driver of biological evolution. As such, bioenergetics offers insight into questions about the evolutionary history of phylogenetic lineages, including recent changes within our own. Subtle differences between archaic and modern humans in terms of body size, shape, and development would have had important ramifications in terms of energy budgets and the potential to invest in reproduction. These energetic differences should thus provide a key to understanding how modern humans were ultimately able to out-compete their archaic counterparts. Furthermore, many of the anatomical changes that accompanied the evolution of modern humans may be linked to a reduction in energetic demands.

While the first studies of organismal energy expenditure date back to the mid-nineteenth century (Sarrus and Rameaux, 1839, cited in McNab, 2002), paleoanthropology has only recently embraced this perspective (Leonard and Ulijaszek, 2002), especially as applied to differences between archaic and modern humans. For instance, the previous edition of this book (Smith and Spencer, 1984) did not include a chapter dedicated to energetics, incorporating only brief suggestions by Smith (1984) and Trinkaus (1984b) that the massive bodies of archaic humans would have been energetically costly. Meanwhile, those authors posited that advances in technology might have allowed modern humans to reduce their muscularity

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and skeletal robusticity, resulting in decreased energetic requirements and conveying a selective advantage. Although Smith and Trinkaus elaborated on this idea elsewhere (Trinkaus, 1981, 1983a,b, 1984a, 1986, 1987b; Smith, 1985; Trinkaus and Smith, 1985; Smith et al., 1989; Smith and Trinkaus, 1991), most formal work on energetics contemporaneous with the book's earlier edition focused on the origin of hominins (e.g., Rodman and McHenry, 1980; Martin, 1983; Carrier, 1984). An increased focus on the role of energy in human evolution emerged in the 1990s (e.g., Foley and Lee, 1991; Foley, 1992; Wheeler, 1991, 1992, 1993; Leonard and Robertson, 1992, 1994, 1997a; Steudel, 1994, 1996; Aiello and Wheeler, 1995; Martin, 1996). Only in the past decade, however, have researchers begun to formally address taxonomically narrower problems such as bioenergetic differences between modern humans and Neandertals (Sorensen and Leonard, 2001; Steegmann et al., 2002; Aiello and Wheeler, 2003; Churchill, 2006; Froehle and Churchill, 2009), along with their broader behavioral (MacDonald et al., 2009) and adaptive (Snodgrass and Leonard, 2009) consequences.

Given inherent relationships between anatomy, energy physiology, and reproductive capacity, researchers have multiple lines of evidence from which to compare archaic and modern human characteristics. The relative youth of fossil human bioenergetics, however, limits the available data; therefore we rely, in large part, on our own energetic estimates throughout this chapter. We focus first on three major areas of differentiation for which the most reliable fossil evidence exists: body size, locomotor anatomy, and childhood growth rates. Indicators of all of these factors preserve reasonably well in the fossil record (as compared to, say, aspects of foraging behavior) and carry relatively clear-cut implications for energy expenditure. Using these data, we present a case study comparing early modern humans to Neandertals to illustrate the reproductive consequences of energetic differentiation. Using a variety of methodological approaches, every study on the topic to date agrees that Neandertals would have had substantially higher energy demands, and thus tighter energy budgets, than early modern humans (Sorensen and Leonard, 2001; Steegmann et al., 2002; Aiello and Wheeler, 2003; Churchill, 2006; Froehle and Churchill, 2009; Snodgrass and Leonard, 2009). If these studies are correct, this has potentially important implications for anatomy (in particular relating to the respiratory system), life history, and reproductive rates in the two groups, which we explore more fully here. When considering the topic of modern human origins broadly, this case study's focus is admittedly narrow in both geographic and temporal terms. Nonetheless, Neandertals, as a closely related sister species, provide an appropriate foil for identifying the derived anatomical, physiological, and behavioral features that may have made the modern human form energetically advantageous relative to archaic phenotypes. Before exploring these topics in detail, however, we summarize some key concepts in the study of energy ecology that we use throughout the chapter.

Energy, Reproduction, and Evolution

On a very basic level, the individual organism acts as a medium through which genes accumulate sufficient energy and matter to self-replicate (Dawkins, 1976; Calder, 1984; Ellison, 2003; Wallace, 2010). Consequently, the ability to direct energy to reproduction acts as a driving or limiting factor in evolution. The field of bioenergetics treats organisms as energy input-output systems that favor minimization of individual energy expenditure coupled with maximization of energy directed toward reproduction, within functional, ecological, and phylogenetic limits (Williams, 1966; McNab, 2002). The close relationship between energy availability and reproduction means that changes in energy distribution can directly affect selective fitness and that the imperative to meet reproductive energy requirements constrains the emergence of novel traits (Williams, 1966; McNab, 2002; Wells, 2002; Ellison, 2003). Modeling the interaction between energy, reproduction, and evolution relies upon three key concepts (see Ulijaszek, 1995; McNab, 2002): *energy budgets*, *energy balance*, and *trade-offs*.

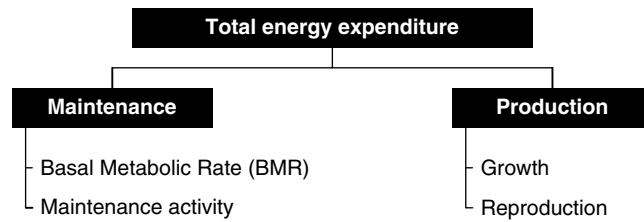


Figure 8.1. Energy budget categories, adapted from Leonard et al. (2007) and Leonard and Ulijaszek (2002).

Energy budgets (Figure 8.1) provide a useful, albeit sometimes overly reductive (McNab, 2002), way to subdivide and categorize gross energy expenditure into smaller, measurable units. The energy budget framework aids in the evaluation of competition for limited resources between different traits or systems, and most budgetary schemata make a primary division between *maintenance* and *production*. Maintenance includes energy for basic life functions and tissue turnover, as well as physical activity, while production includes growth to maturity and the direct costs of reproduction (i.e., energy needs of dependent offspring). In terms of our three main foci in the fossil record, the maintenance category subsumes the energy costs associated with adult body size and locomotion, while energy for development (gestation, lactation, and postweaning growth) falls under production.

The concept of energy balance centers on an individual's ability to meet or exceed requirements through resource acquisition. Acquired energy in excess of maintenance demands (positive energy balance) can then fund reproduction directly by promoting fertilization and offspring nutrition (Ellison, 2003), or indirectly as growth to adult body size and attainment of sexual maturity (Key and Ross, 1999), as well as investment in fat stores against future calorie shortfalls or, in females, for reproduction. Negative energy balance, or a failure to meet maintenance needs, on the other hand, can hamper growth and fecundity (Bogin et al., 2007; Ellison and O'Rourke, 2000; Ellison, 2003). This does not mean, however, that individuals must maintain positive energy balance on a consistent, daily basis. Over a lifetime, rather, sufficient resources above individual maintenance needs should fund a sufficient, population-specific reproductive effort (Vitzthum, 2009) in order to maintain relative fitness.

Trade-offs are shifts in energy allocation between different budget subcategories as a result of anatomical, behavioral, or life history changes in response to environmental stressors (Stearns, 1992). Such alterations in patterns of energy allocation should maximize reproductive potential under specific circumstances. Trade-offs can refer to behavioral (short-term, individual) or evolutionary (long-term, population-wide) compromises between components of energy expenditure and intake, and the devotion of energy to reproduction. The diversity of life in many ways reflects the various energetic trade-offs that populations have made over evolutionary time, resulting in a vast assortment of successful energy acquisition and allocation patterns. Much of the differentiation within the primate order relates to variability in energetic strategies (e.g., strepsirhines: Kurland and Pearson, 1986; Wright, 1999; Schmid, 2000; Genoud, 2002; Snodgrass et al., 2007; callitrichids: Sussman and Kinzey, 1984; Sanchez et al., 1999; Bales et al., 2000; Schradin and Anzenberger, 2001a,b; Fite et al., 2005; highly folivorous monkeys: Korstjens et al., 2010), and humans are no exception. The evolution of derived human traits, including body size, locomotor habits, subsistence behavior, and developmental and reproductive patterns, all likely involved trade-offs between energy budget categories that diverge from our last common ancestor with panins (Rodman and McHenry, 1980; Carrier, 1984; Hawkes et al., 1989, 1997; Leonard and Robertson, 1992, 1994, 1997a;

Aiello and Wheeler, 1995; Steudel, 1996; Bogin, 1997, 2006; Sear et al., 2000; Aiello and Wells, 2002; Bramble and Lieberman, 2004; Kramer, 2005; Hrdy, 2009; Reiches et al., 2009). Trade-offs in energy allocation can be necessary to accommodate the energy demands of novel, advantageous traits (e.g., larger brains) when maintenance energy budgets are constrained by the imperative to maintain energy balance favorable to reproduction. It may also be possible in some cases that reductions in energy expenditure can promote increases in fertility rates if they *reduce* maintenance costs over a given period of time, potentially freeing up additional energy for reproduction. Differences between archaic and modern humans likely fall into this latter category in that, as we show below, many modern aspects of anatomy likely translated into lower adult maintenance costs. What, then, were the specific energetic effects of archaic versus modern human anatomy?

Maintenance

Body Size and Energy Expenditure

Body size is perhaps the most important factor in the study of physiological evolution, since complex interactions between mortality risk, nutritional availability, population density, metabolic physiology, and reproduction relate to environment-specific body size variation within a species or in closely related taxa (for comprehensive reviews, see Peters, 1983; Schmidt-Nielsen, 1984; Calder, 1984; McNab, 2002; Bernstein, 2010). Especially critical to the study of bioenergetics, body size correlates with variables from all subcategories of energy expenditure (see Figure 8.1) within and across species, including the energetic costs of tissue maintenance, locomotion, gestation and lactation, and growth to maturity (Ulijaszek, 1995). In addition to these subcategories, body size also correlates roughly with total free-living daily energy expenditure (DEE). Recent methodological advances (Prentice, 1990; Butler et al., 2004) have led to the accumulation of a taxonomically diverse sample of DEE data from animals in the field, analysis of which shows significant correlations between DEE and body size (Nagy, 1987, 1994; Nagy et al., 1999). Given the wide array of influences on inter-individual and interspecific variation in energy expenditure (many of which may not be reflected in the fossil and archaeological records), however, body size by itself does a poor job of explaining variation in DEE (McNab, 2002). Moreover, the use of body size in isolation to estimate DEE masks potential differentiation among archaic and modern humans in other more specific subcomponents of energy expenditure. In fact, the impact of variation in these subcomponents on reproductive rates is the central focus of this chapter.

The major component of DEE is basal metabolic rate (BMR)—the energy required for basic physiological functions, excluding digestion. Variation in body mass explains ~72% of variation in BMR across mammals (Capellini et al., 2010), and roughly 80% of variation across large and geographically diverse samples of humans (Henry, 2005; Froehle, 2008). Because of this strong positive correlation, BMR is probably the most widely studied energy expenditure variable and provides the basic foundation upon which current understanding of the body size/energy relationship stands. In terms of fossil hominins, where body mass can be estimated relatively reliably, BMR provides a baseline estimate of maintenance energy expenditure to which estimates of other energy costs can be added.

In endotherms, BMR scales allometrically with body mass (Brody and Procter, 1932; Kleiber, 1932, 1961; Benedict, 1938), as expressed by the commonly used Kleiber (1961: 212) equation:

$$\text{BMR} = 70 \cdot M_b^{0.75},$$

where M_b is body mass in kg and BMR is in kilocalories per day (kcal/d). (Note that a large volume of recent work reconsiders the specific exponent of the body mass/BMR relationship and its underlying physiological mechanisms, but is beyond the scope of the present chapter. For more information, see Heusner, 1982a,b; West et al., 1997; Hulbert and Else, 1999, 2000; West, 1999; McNab, 2002, 2008; White and Seymour, 2003; West and Brown, 2004; Capellini et al., 2010; Clarke et al., 2010; Isaac and Carbone, 2010; Kolokotronis et al., 2010.) Humans and chimpanzees generally conform to expectations from the Kleiber equation, both species falling on average within 3–7% of expected values (Froehle and Schoeninger, 2006). In concert with the wide geographical range of the human species, however, climate appears to underlie significant variation in human BMR, and some populations deviate more than others from Kleiber's expected values (Roberts, 1978; Henry and Rees, 1991; Leonard et al., 2002, 2005; Froehle, 2008). This is potentially important for comparisons between hominins inhabiting different ecogeographical regions (e.g., Froehle and Churchill, 2009).

The relationship between body size and BMR is integral to the energetic analysis of modern human origins, primarily because the emergence of *Homo sapiens* appears to have been accompanied by a significant reduction in body mass (Ruff et al., 1997; Churchill et al., 2012). Table 8.1 presents body mass estimates for samples of *H. heidelbergensis*, *H. neanderthalensis*, and early *H. sapiens*. Although body composition, especially body fat content, affects estimates of BMR (Cunningham, 1980, 1991), it is difficult to ascertain fat percentage in fossil specimens; thus our fossil body mass estimates assume body composition similar to the recent humans from which the BMR predictive equations derive. This probably slightly underestimates fossil BMR, since fat has a much lower metabolic rate at rest than other tissues such as skeletal muscle (cf. Aschoff et al., 1971; Simonsen et al., 1994), and foragers likely maintain lower body fat than the largely sedentary samples used to generate predictive equations for BMR (e.g., the Hadza; Sherry and Marlowe, 2007). This estimation bias, however, applies uniformly across all of our fossil samples, and thus should not affect our results.

The data in Table 8.1 show reduced body mass in early *H. sapiens* when compared to *H. heidelbergensis* and *H. neanderthalensis* (see also Figure 8.2). Within males, these differences reach statistical significance (one-way ANOVA, $P < 0.01$) and the data sort into three groups (Waller-Duncan, k -ratio=100): archaic humans (*H. heidelbergensis* and Neandertals: $N=7$, mean=79.3 kg; and $N=9$, mean=76.9 kg, respectively), early anatomically modern humans (early [EUP] and late [LUP] Upper Paleolithic: $N=11$, mean=68.1 kg; $N=23$, mean=67.1 kg, respectively), and recent humans from small-scale societies (see Table 8.2; grand mean of twenty-seven groups=56.7 kg). Female groups also differ significantly for body mass (one-way ANOVA, $P < 0.01$), but sort differently and less clearly into two groups (Waller-Duncan, k -ratio=100): one grouping consists of all modern humans (EUP: $N=7$, mean=59.6 kg; LUP: $N=14$, mean=58.0 kg; recent: grand mean of twenty-seven groups=49.1 kg), while the other includes all fossil groups (*H. heidelbergensis*: $N=2$, mean=60.4 kg; *H. neanderthalensis*: $N=6$, mean=66.6 kg; EUP and LUP as above). The discrepancy between male and female results probably stems at least in part from the females having smaller sample sizes coupled with within-group variance similar to that of the males.

Despite the inconsistencies between males and females, the observed trends in body size have important implications for BMR in these groups. Following the groupings derived from the male-specific ANOVA results (and ignoring climate for the time being), we would expect archaic human males to have average BMR of 1791 kcal/d (using the Oxford-Brookes BMR database equations for ages 18–30 years; Henry, 2005), which translates to 373 L O_2 /d using the conversion factor of 4.8 kcal/L O_2 . Predicted EUP and LUP modern human BMR is ~9% lower at 1624 kcal/d (338 L O_2 /d), while in recent subsistence-level men the average falls to 1453 kcal/d (303 L O_2 /d), or about 18% less than the archaic human mean. For females, archaic, early modern, and recent women have predicted BMR values of 1410 kcal/d (294 L

Table 8.1. Body mass, basal metabolic rate, and cost of transport estimates for archaic and early modern humans.

Species/Group	Specimen	Mass (kg) ^a	BMR (kcal/d) ^b	Cost of Transport (mL O ₂ /m) ^c
<i>Homo heidelbergensis</i> (600–300 kya)	Males			
	Arago 44	79.2	1812	–
	Atapuerca Pelvis 1	85.9 ^d	1919	–
	Atapuerca AT-800	74.0 ^d	1729	–
	Atapuerca AT-835	76.3 ^d	1766	–
	Atapuerca AT-2350	74.0 ^d	1729	–
	Berg Aukas	92.0 ^e	2017	–
	Broken Hill E.719	73.6	1723	–
	Male Mean	79.3	1814	–
	Females			
	Atapuerca Coxal I	55.4 ^d	1284	–
	Atapuerca AT-1004	65.3 ^d	1413	–
	Female Mean	60.4	1349	–
	Sex Uncertain			
	Broken Hill E.689	73.8	1625	–
	Broken Hill E.907	80.6	1724	–
	Overall Mean	75.5	1704	–
<i>Homo neanderthalensis</i> (150–45 kya)	Males			
	Amud 1	70.3	1670	10.1
	Kebara 2	75.6	1755	–
	Krapina 213	80.6	1835	–
	La Ferrassie 1	85.0	1905	14.2
	La Chapelle 1	77.3	1782	13.4
	Neandertal 1	78.9	1807	–
	Shanidar 4	72.0	1697	–
	Shanidar 5	68.5	1641	10.8
	Spy 2	83.6	1883	15.1
	Male Mean	76.9	1775	12.7
	Females			
	Grotte du Prince	74.8	1538	–
	Krapina 208	68.4	1454	–
	Krapina 209	63.7	1392	–
	Krapina 214	62.6	1378	–
	La Ferrassie 2	67.0	1436	11.9
	Tabun C1	63.2	1386	–
	Female Mean	66.6	1430	11.9
	Overall Mean	72.8	1637	12.6

Table 8.1 (Continued)

Species/Group	Specimen	Mass (kg) ^a	BMR (kcal/d) ^b	Cost of Transport (mL O ₂ /m) ^c
<i>Homo sapiens</i> Skhūl-Qafzeh (98–90 kya)	Males			
	Skhūl 4	70.3	1670	8.5
	Skhūl 5	67.6	1627	8.6
	Male Mean	69.0	1649	8.6
	Females			
	Qafzeh 9 ^f	63.2	1386	8.2
	Female Mean	63.2	1386	8.2
	Overall Mean	67.0	1561	8.4
	Males			
	Arene Candide 1 (IP)	66.4	1607	10.6
<i>Homo sapiens</i> Early Upper Paleolithic (33–20 kya)	Barma Grande 2	80.7	1836	11.6
	Nazlet Khater 1	52.2	1380	–
	Kubbaniya	69.6	1659	–
	Mladeč 21	62.7	1548	–
	Cro Magnon 1	67.6	1627	10.1
	Grottes des Enfants 4	83.8	1886	12.2
	Dolní Věstonice 14	72.0	1697	10.4
	Předmostí 3	70.8	1678	10.4
	Předmostí 14	65.9	1599	10.2
	Paviland	72.9	1711	11.3
	Caviglione	65.2	1588	9.7
	Male Mean	69.2	1652	10.7
	Females			
	Grottes des Enfants 5	52.8	1250	7.9
	Dolní Věstonice 3	54.8	1276	8.8
	Předmostí 1	55.4	1284	–
	Předmostí 4	65.1	1411	11.1
	Předmostí 9	57.7	1314	9.0
	Předmostí 10	70.6	1483	12.6
	Paglicci 25	60.6	1352	–
	Female Mean	59.6	1339	9.7
	Sex Uncertain			
	Cro Magnon 2	59.2	1413	8.2
	La Rochette 1	64.7	1493	10.2
	Mladeč 22	76.5	1665	–
	Overall Mean	65.8	1534	10.3

(Continued)

Table 8.1 (Continued)

Species/Group	Specimen	Mass (kg) ^a	BMR (kcal/d) ^b	Cost of Transport (mL O ₂ /m) ^c
<i>Homo sapiens</i> Late Upper Paleolithic (20–10 kya)	Males			
	Arene Candide 2	67.7	1628	11.6
	Arene Candide 4	71.6	1691	12.2
	Arene Candide 5	68.7	1644	11.5
	Arene Candide 10	68.7	1644	11.8
	Bichon 1	58.4	1479	9.1
	Chancelade	64.5	1577	–
	Grotta Continenza	68.1	1635	12.2
	Grotte des Enfants Mes.	51.5	1369	–
	Jebel Sahaba 117–5	65.2	1588	8.0
	Jebel Sahaba 117–10	63.1	1555	8.3
	Jebel Sahaba 117–18	70.8	1678	10.5
	Jebel Sahaba 117–19	61.7	1532	–
	Jebel Sahaba 117–29	73.1	1715	–
	Jebel Sahaba 117–39	65.7	1596	9.9
	Jebel Sahaba 117–40	65.0	1585	–
	Minatogawa 1	60.3	1510	11.1
	Neuessing 2	70.8	1678	11.9
	Oberkassel 1	72.4	1703	11.7
	Ohalo 2	73.5	1721	12.1
	Parabita 1	73.3	1718	11.2
	Romito 3	72.7	1708	11.6
	Veyrier 1	56.2	1444	7.6
	Male Mean	66.5	1609	10.7
	Females			
	Bruniquel 24	60.1	1345	9.8
	Cap Blanc 1	57.8	1315	9.4
	Jebel Sahaba 117–6	65.3	1413	–
	Jebel Sahaba 117–22	60.1	1345	–
	Jebel Sahaba 117–26	53.6	1260	7.8
	Jebel Sahaba 117–28	54.5	1272	–
	Minatogawa 2	45.9	1159	–
	Minatogawa 3	50.2	1216	9.2
	Minatogawa 4	47.4	1179	8.9
	Oberkassel 2	56.8	1302	–
	Parabita 2	69.7	1471	10.9
	Romito 4	60.4	1349	9.9
	San Teodoro 4	68.2	1451	–
	St. Germain-la-Rivière	61.5	1364	10.8
	Female Mean	58.0	1318	9.6

Table 8.1 (Continued)

Species/Group	Specimen	Mass (kg) ^a	BMR (kcal/d) ^b	Cost of Transport (mL O ₂ /m) ^c
Sex Uncertain				
	Arene Candide 1a	75.4	1649	–
	Jebel Sahaba 117–1	66.5	1519	–
	La Madeleine	66.7	1522	–
	Laugerie Basse	81.7	1740	–
	Placard 16	66.5	1519	–
	Overall Mean	64.2	1507	10.4

^aBody mass estimation techniques contain inherent error, but different techniques (e.g. femoral head diameter vs. bi-iliac breadth + stature) provide largely concordant results, suggesting that the estimates are at least reasonable, or biased in the same manner. Given that existing techniques will underestimate mass in some individuals while overestimating it in others, it is unwise to place a great deal of confidence in an estimate derived for any given individual. Assuming, however, that the error is random with respect to taxonomic group, the central tendencies of the estimates should be reasonable reflections of sex-specific, species-average mass. Additionally, sex attribution in fossil individuals is difficult, and misattribution of sex can confound estimates of sex-specific mass, especially where sample sizes are small. This is a problem inherent in human paleontological research generally and is not unique to this study. With these caveats in mind, we have included fossil mass estimates from the supplemental data from Ruff et al. (1997) unless otherwise noted. To estimate body mass, Ruff et al. used methods that rely upon femoral head diameter or on stature and bi-iliac breadth, or the average of these two methods. In many specimens, femoral head diameter was estimated from acetabular height. On the recommendation of Auerbach and Ruff (2004), we omitted specimens from the Ruff et al. (1997) sample for which bi-iliac breadth could not be measured directly. We also omitted juveniles, specimens with an unclear taxonomic association, and modern human specimens that have proven to be more recent than initially thought.

^bBasal metabolic rate estimates calculated using sex-specific equations for adults aged 18–30 years (Henry, 2005). For individuals with uncertain sex, BMR values are the average of male and female estimates.

^cCost of transport estimates calculated using body mass and lower limb length following Steudel-Numbers and Tilkens (2004). See text for more details.

^dEstimate derived from acetabular height value published in Arsuaga et al. (1999). Femoral head diameter for these specimens was estimated using a formula provided in Rosenberg et al. (2006). Body mass estimates were then calculated using the average of the three femoral head diameter formulae presented in Ruff et al. (1997). The femoral head diameter estimate for Atapuerca Pelvis 1 was further averaged with the stature and bi-iliac breadth estimate published by Arsuaga et al. (1999) to provide the estimate presented here. Our estimates for these specimens differ slightly from those published in Rosenberg et al. (2006), who based their estimation on only two of the femoral head diameter formulae from Ruff et al. (1997). However, as the rest of the estimates presented here are based on all three formulae, we followed the same method in order to maintain consistency.

^eEstimate derived from femoral head diameter (Grine et al., 1995) using the average of the three formulae from Ruff et al. (1997). Berg Aukas was presumably omitted from the Ruff et al. sample due to issues raised in Trinkaus et al. (1999). However, see Churchill et al. (2012) for a contrary view and our justification for including this specimen.

^fIn designating Qafzeh 9 as female, we follow Vandermeersch (1981; Bruzek and Vandermeersch, 1997), although others classify this specimen as male (e.g., Wolpoff et al., 2001).

O₂/d), 1324 kcal/d (or 276 L O₂/d, ~7% lower than archaic females), and 1201 kcal/d (or 250 L O₂/d, ~15% lower than archaic females), respectively. On the basis of mass alone, the archaic/early modern human difference in BMR is of a similar magnitude to the difference between the relatively heavy U.S. population and smaller-bodied recent populations from developing countries (from data compiled in Froehle, 2008).

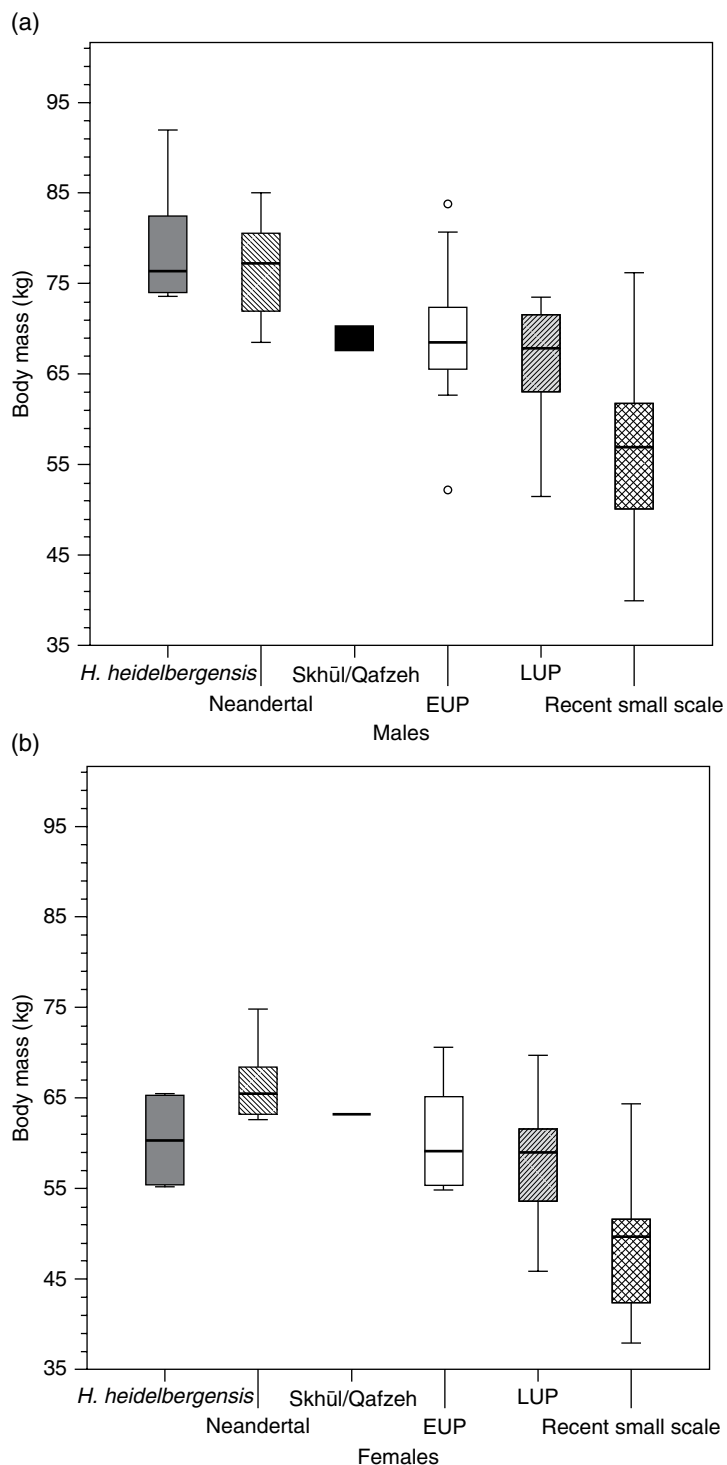


Figure 8.2. Distribution of body size estimates in archaic and modern fossil humans, as well as recent humans from small-scale societies. Data and references are in Table 8.1 (fossils, not including “sex-uncertain” individuals) and Table 8.2 (recent small-scale groups). Fossil plots are derived from data on individuals (male N: *H. heidelbergensis*=7; Neandertals=9; EUP=11; LUP=23; female: *H. heidelbergensis*=2; Neandertals=6; EUP=7; LUP=14), while data for recent groups consist of twenty-seven population means.

Table 8.2. Body mass in small-scale societies.

Group	Mean Body Mass (kg) ^a	
	Males	Females
Ache	59.8	53.7
Aeta	40.0	38.0
Agta	46.4	40.3
Arnhem Land	55.5	41.3
Asmat Baka	49.6	47.2
Batak	46.9	40.8
Buryat ^b	67.2	60.2
Evenki ^b	55.3	52.0
Gainj and Asai	43.3	38.0
Guaja	61.1	50.4
Hadza	54.0	48.0
Hiwi	57.4	49.7
Inuit ^c	65.5	61.2
Ju'/'hoansi	50.6	42.2
Ket ^b	62.3	50.1
Machiguenga	62.2	51.0
Maku-Nadeb	60.6	49.7
Maya	60.3	51.3
Pygmy (East)	43.0	39.4
Pygmy (West)	48.3	42.7
Sakha (Yakut) ^d	66.6	60.4
Toba	76.3	64.2
Tsimane	61.3	51.0
Turkana	55.6	48.9
Walbiri	57.0	45.0
Wichi	73.9	62.3
Yanomamo	52.0	45.4
Overall Mean	56.7	49.1

^aData from Walker et al. (2006) unless otherwise noted.^bLeonard et al. (2005).^cRode and Shephard (1995).^dSnodgrass et al. (2005).

Incorporating the effects of climate leads to even larger potential differences between geographically widely separated populations, both within and between hominin groups. Using climate-based BMR equations derived from a large sample of recent humans (Froehle, 2008), and relying on mean annual temperatures from that dataset, we would predict, for example, that modern human LUP females living in tropical areas would require ~1290 kcal/d (269 L O₂/d), compared to ~1400 kcal/d (292 L O₂/d, ~8% higher) for females of the same body size living in circumpolar or peri-glacial regions. Even greater differences can occur when both climate and body size differences contribute to the estimates: the average late-surviving Neandertal male in Europe might have a BMR of about 1840 kcal/d (383 L O₂/d), while his

anatomically modern contemporaries in sub-Saharan Africa would require only ~1600 kcal/d (333 L O₂/d), or about 14% less energy.

Differences in BMR due to climate or body size are particularly important when attempting to estimate DEE for fossils. This is because other energy costs, especially those related to physical activity, are neither observable nor reliably quantifiable from data preserved in the archeological or fossil record. Instead, estimates of fossil DEE employ the factorial method (see Leonard et al., 1997; Froehle, 2008; Froehle and Churchill, 2009), which accounts for gross activity energy expenditure by multiplying BMR by a physical activity level (PAL) coefficient. Active to moderately active individuals generally have PAL values between 1.7 and 1.99 times BMR, while vigorously active individuals have PAL > 2.0 (FAO, 2004). Thus, in the absence of more detailed behavioral data, DEE estimates using the factorial method simply magnify variation in BMR on the basis of a few rough ecological correlates of subsistence activity (e.g., primary productivity, available biomass). Although the factorial method quite clearly incorporates a considerable degree of error, it is important to minimize such error by accounting for relevant, measureable (or estimable) factors such as body size and climate. Another crucial consideration is the accurate interpretation of activity and locomotor costs in the fossil record in order to best approximate PAL values for extinct groups. Although the task of estimating activity costs in fossil groups presents numerous challenges, comparing some aspects of archaic and modern human anatomy can provide some preliminary clues, which we discuss in the following section.

Locomotor Energetics and Activity Energy Expenditure

While industrialized populations tend to spend a relatively small fraction of total energy on exercise (Hayes et al., 2005), foragers and other small-scale societies often expend 40–50% of daily energy on activity (Godin and Shephard, 1973; Leonard and Robertson, 1992; Katzmarzyk et al., 1994; Yamauchi et al., 2000). Assessing activity energy expenditure in the fossil record relies on the combination of evidence from modern exercise physiology and fossil anatomy, as well as pairing the study of extant hunter-gatherers with archaeological and bioarchaeological evidence for fossil technology, subsistence behavior, and diet.

Locomotor energy costs constitute a large portion of activity energy expenditure in most humans that hunt and gather for subsistence. Of course, activity energy expenditure involves more than simply locomotion, and variation in hunting and gathering behavior patterns can impact energy expenditure. Measuring or even estimating activity energy expenditure in extant, free-living foragers, however, proves rather difficult, even with detailed behavioral observations (Leonard, 2003). Pinning down the specific behaviors in which fossil populations engaged is considerably more difficult, and thus extending the scant evidence for specific behaviors to energy estimates is even less reliable. Thus we are constrained to focus on locomotor costs as the major part of the forager activity budget and to make gross estimates of the overall energetic costs of activity in extinct groups.

Large day ranges and central-place foraging, where foragers set out from and return to the same camp in a single day (O'Connell et al., 1988, 1990; Cashdan, 1992; Marlowe, 2005; as opposed to much shorter, one-way foraging trips in apes; e.g., Wrangham and Smuts, 1980; Herbinger et al., 2001; Pontzer and Wrangham, 2004), lead to considerable energy expended on travel in hunter-gatherers (Leonard and Robertson, 1992, 1997a, b). From data on the Ju'hoansi (!Kung) and Ache compiled in Leonard and Robertson (1997a), daily travel accounts for 45–50% of foraging activity energy expenditure. The seasonality of hunter-gatherer diets (see below) also leads in most cases to at least some degree of nomadic migration throughout large home ranges over the course of the year (Hill et al., 1984; Cane, 1987; Kuchikura, 1988; Kelly, 1995). This makes efficiency important in order to minimize the energy costs of such extensive travel.

The fossil record preserves skeletal indicators of efficiency, allowing for some comparisons between hominins. The major determinants of the energetic cost of vertebrate locomotion include body size and speed of travel (Taylor et al., 1970, 1982; Waters et al., 1988; Steudel-Numbers and Tilkens, 2004; Steudel-Numbers and Wall-Scheffler, 2009), while the biomechanical properties associated with variation in anatomical traits such as limb length also modify these relationships (Dawson and Taylor, 1973; Tucker, 1975; Parsons and Taylor, 1977; Sherman, 1998; Steudel-Numbers and Tilkens, 2004; Kramer and Sarton-Miller, 2008). Carrying loads (whether food or children) also increases the energy cost of travel since load-bearing adds to the total mechanical work performed (Kramer, 1998, 2010; Wall-Scheffler et al., 2007; Watson et al., 2008). To gauge differences between archaic and modern humans in locomotor energy requirements we will evaluate variation in the *cost of transport*, which is the energy expended in movement per unit distance, and as such is a measure of *locomotor economy*, or the amount of energy expended required to accomplish a specific task (terminology following Cavanagh and Kram, 1985; Steudel, 2000; Kramer and Sylvester, 2009).

In terms of *locomotor efficiency* (which refers to the amount of physical work accomplished in movement, divided by the energy expended to accomplish that work), bipedal walking affords humans an energetic advantage over the locomotor behaviors of many other primates (Steudel-Numbers, 2003), including chimpanzees walking or running quadrupedally or bipedally (Taylor and Rowntree, 1973; Sockol et al., 2007). While the advantages of human walking over quadrupedal movement are speed-dependent (Leonard and Robertson, 1995), distance covered per unit time is also important, and modern humans appear rather adept at covering large daily distances relatively efficiently. Most work related to locomotor energetic deals with the origin of bipedality or the relative efficiency/economy of early hominins (Rodman and McHenry, 1980; Leonard and Robertson, 1995; Kramer, 1999; Kramer and Eck, 2000; Wang et al., 2004; Nagano et al., 2005; Sellers et al., 2005; Pontzer et al., 2009a). Although debate remains (e.g., Lovejoy 2005a,b, 2007), the preponderance of evidence suggests that pre-*Homo* hominins would have used more energy to move the same distance at the same speed as anatomically modern humans. Archaic humans, meanwhile, share basic locomotor kinematics with modern humans but may nonetheless have moved less economically or had slower optimal speeds, for reasons of body size and shape.

Within recent humans, a number of factors influence the energetic economy of locomotion: for example, each individual has his or her own optimal walking speed, where the energy cost of moving a certain distance is minimized (Ralston, 1976; Anderson and Pandy, 2001). Anatomical variation appears to underlie interindividual differences in locomotor costs and optimal walking speeds. While stature, aside from its association with body mass, does not affect walking costs (Censi et al., 1998), lower limb length does seem to have important effects: relative to body mass, humans with longer lower limbs have reduced walking cost of transport (Steudel-Numbers and Tilkens, 2004; Kramer and Sarton-Miller, 2008). These findings may relate to greater stride length in longer-legged people, leading to less muscle exertion required to maintain posture (Alexander, 1991; Polk, 2004) and perhaps lower ground force generation during stance phase (Kram and Taylor, 1990; Griffin et al., 2003; Pontzer, 2005, 2007a,b).

Gruss (2007) showed that longer lower limbs experience greater anterior-posterior bending stress in the femoral and tibial diaphyses, leading to compensation in the form of a more extended knee during later stance phase. This postural difference may lessen the amount of muscular force required to resist gravity, such that longer-limbed people use less energy than shorter-limbed people (Alexander, 1991; Polk, 2004; Pontzer, 2005; Gruss, 2007). Interestingly, in contrast to overall lower limb length, crural index does not affect locomotor costs (Steudel-Numbers and Tilkens, 2004). Also, despite the upper limb's participation in human movement, restricting upper limb swing apparently has very little influence on the metabolic costs of walking or running (Wall-Scheffler et al., 2007; Pontzer et al., 2009b). Thus, in evaluating archaic and

modern human locomotor energy expenditure, we will consider only the biomechanical effects of lower limb length along with the influence of body size on mechanical work performed.

Relying on experimental data from recent humans, Steudel-Numbers and Tilkens (2004) provide a single equation to account for the effects of both body mass and leg length on cost of transport in bipedal hominins when speed is held constant:

$$\text{Cost of transport (mL O}_2\text{/m)} = 8.301 + (0.234 * M_b) - (0.169 * \text{LLL}),$$

where M_b is body mass in kg and LLL is lower limb length in cm. This equation provides estimates of the cost of movement only, excluding additional costs for bodily maintenance during the period of movement. Those authors applied that equation to fossil specimens, indicating that at the same speed, Neandertals ($N=6$) would have required 12.4 mL O_2 for every meter traveled, while early modern humans ($N=6$) would have used only about 8.5–9.0 mL O_2 /m, or about 30% less energy. Following up on that work, Weaver and Steudel-Numbers (2005) used limb length together along with body mass to account for locomotor and maintenance energy costs simultaneously. They estimated that on average, Neandertals would have spent ~215 kcal/d more than early modern humans to cover the same distance.

Adding limb length measurements and estimates from the literature (Holliday, 1995; Porter, 1999; Shackelford, 2005) to our body mass database, we made similar calculations of cost of transport in an expanded sample (see Table 8.1). Unfortunately, this precluded us from evaluating *H. heidelbergensis* due to a lack of femur and tibia lengths from the same individuals. Our results are broadly consistent with those of Steudel-Numbers and Tilkens (2004) and Weaver and Steudel-Numbers (2005), although differences are of a slightly lesser magnitude. Once again holding speed constant, our sample predicts an average cost of transport of 12.6 mL O_2 /m in Neandertals ($N=6$), 10.2 mL O_2 /m in early Upper Paleolithic modern humans ($N=15$; only European specimens had measurable LLL), and 10.4 mL O_2 /m in late Upper Paleolithic modern humans ($N=26$; European, North African, West and East Asian specimens). Unsurprisingly, given slight sexual dimorphism, males of all fossil groups have moderately higher locomotor costs than females (by 7–13%); within sexes, the Neandertal/modern human differences remain of consistent magnitude.

As opposed to the 30–35% difference in cost of transport estimated by Steudel-Numbers and Tilkens (2004) and Weaver and Steudel-Numbers (2005), our estimates suggest that Neandertals and modern humans only diverged by about 20–24%, both within sexes and when sexes are combined. Still, this magnitude of difference could have had important consequences for energy expenditure and behavioral patterns in these groups of hominins. In caloric terms, Neandertals and early modern humans traveling at the same speed would require about 60 versus 50 kcal/km, respectively. If these hominins moved 15–19 km per day, as male Ache and Ju'/hoansi foragers do on average (data compiled in Leonard and Robertson, 1997a), then the excess cost for Neandertals would be expected to reach 150–200 kcal/d, again assuming comparable walking speeds. Female Neandertals, using Ache and Ju'/hoansi averages of ~9 km per day, would require ~100 kcal more to move the same distance at the same speed as their anatomically modern human counterparts. These differential costs should be seen as minima, since foraging in the cold-temperate environments of glacial Europe likely demanded greater mobility than that of modern neo-tropical (Ache) or subtropical (Ju'/hoansi) foragers.

Differences in limb length and body mass suggest that on average archaic humans were less economical at moving over a given distance than modern humans. If we assume that archaic and modern humans allotted the same absolute number of calories to movement, then this

would likely limit archaic humans to smaller day ranges, reduce their effective foraging radius, and demand greater residential mobility as a means of solving biodepletion issues (Anwar et al., 2007; MacDonald et al., 2009). Conversely, archaic humans may have maintained large home ranges and moved about them above optimal speeds (as expected relative to modern humans in Steudel-Numbers and Tilkens, 2004), simply dealing with the excess energy costs and living with overall greater energy throughput (although such a strategy would likely reduce net caloric return rates below sustainable levels; see Churchill, 2006).

It is worth noting that the adaptive strategies of early modern Europeans, as reflected in both archeologically recovered faunal and artifactual remains, as well as isotopic signatures in human fossils, involved a marked expansion of diet breadth (Stiner et al., 2000; Stiner, 2001; Richards et al., 2001; Richards, 2007, 2009; although debate remains over the isotope data; see Drucker and Bocherens, 2004) accompanied by a florescence of extractive subsistence technology (projectile weaponry, fishing tackle, nets, and possibly traps; see Churchill and Rhodes, 2009; Rhodes and Churchill, 2009; Villotte et al., 2010). This technology had the direct effect of reducing the handling costs of small and relatively hard to capture prey items, making it economically worthwhile to incorporate them into the diet. These items have lower search costs than larger prey (Winterhalder and Smith, 1981), and thus the Upper Paleolithic expansion of diet breadth was likely tied to a substantial reduction in the mobility costs of foraging. This, along with the inherently higher price per step paid by the Neandertals, must have translated into marked differences in foraging costs, net return rates, and ultimately, energy budgets between groups. Indeed, even conservative estimates of daily energy expenditure in Neandertals fall at the upper end of the range for recent foraging populations (Sorensen and Leonard, 2001).

Finally, recently renewed interest in the role of running in human evolution (e.g., Bramble and Lieberman, 2004; Rolian et al., 2009; Lieberman et al., 2010) merits brief discussion here, although comparisons between archaic and modern humans for endurance running capabilities are currently limited. Human running is exceptionally energetically expensive in comparison to other mammals and is about twice as costly as human walking (Margaria et al., 1963; Taylor et al., 1982; Carrier, 1984; Sherman et al., 1998). Although several aspects of modern human anatomy may help minimize the cost of transport in long-distance running (Alexander, 1991; Carrier, 1984; Myers and Steudel, 1985; Larsen, 2003; Bramble and Lieberman, 2004; Lieberman et al., 2006, 2010; Steudel-Numbers et al., 2007; Rolian et al., 2009), this activity nonetheless incurs high energy demands, potentially limiting its utility as a routine foraging strategy (Bramble and Lieberman, 2004; Lieberman et al., 2007; Pickering and Bunn, 2007; Steudel-Numbers and Wall-Scheffler, 2009). With specific regard to modern human origins, limited work suggests that archaic humans may have run even less efficiently than do modern humans (e.g., Raichlen, 2011), but far more data is needed before this is confirmed. Anatomical variation may have made the decision as to when to run different in archaic versus modern humans, but in both cases, the energy costs of such behavior would have been extremely high.

Production: Energy for Offspring Growth and Development

To this point, we have only discussed energy expenditure on the “Maintenance” side of the energy budget (Figure 8.1), and only in adults. From a biological standpoint, however, all of that maintenance is basically useless if it does not allow the diversion of sufficient energy to reproduction, the major component of the “Production” side. The ability to produce more offspring depends upon energy availability in any species, but humans appear exceptionally needy. Human offspring are particularly “expensive” for a variety of reasons. Human neonates are born with brains 50% larger for their bodies than are apes, and they maintain the

high fetal rate of brain growth for a full year postnatally, while other primates reduce brain growth rates at birth (Martin, 1983, 2007). On the other hand, despite this “head start” in brain growth, somatic maturation overall is delayed in humans compared to panins. While chimpanzees achieve nutritional independence shortly after weaning (Robson et al., 2006), humans have a unique childhood period (Bogin and Smith, 1996; Bogin, 1997, 1999) consisting of several years between weaning and the point in adolescence when humans finally gain the ability to fully obtain their own food. In Hadza hunter-gatherers, for example, children are usually weaned by age 3 years (Marlowe, 2002), and above age 5 years, are even capable of obtaining 50% of their own calories (Blurton Jones et al., 1989, 1994; Marlowe, 2003). Nonetheless, the Hadza and other hunter-gatherers acquire the capacity for full nutritional independence only around age 18 (Hrdy, 2005). Although children do contribute to their own care and to the care of other children in a variety of ways (e.g., by holding infants while mothers forage or process food; Crittenden and Marlowe, 2008), adults still provide a considerable portion of offspring calories before puberty.

Including her own BMR and activity costs, a woman expends roughly 2.5 million kcal during the gestation and lactation periods to raise a single human infant to weaning (Aiello and Key, 2002). This does not include the cost of child carrying, which adds considerably to locomotor energy expenditure (Kramer, 1998; Wall-Scheffler et al., 2007; Watson et al., 2008). The long period from infancy to nutritional independence requires roughly 9–13 million kcal (Hrdy, 2005; Gurven and Walker, 2006), a portion of which juveniles gradually obtain for themselves, but probably at least a third of which must come from provisioning (using rough estimates of age-specific growth rates from Walker et al., 2006, and the aforementioned self-provisioning benchmarks for the Hadza). Considering that humans “stack” births, and thus have to care simultaneously for multiple nutritionally dependent offspring, the compound energy needs of all children at a woman’s reproductive peak are enormous. Data on Ache and Ju’/hoansi foragers show that during her reproductive years, a woman’s dependent children combined require a total of 3000–6500 kcal/d (supplemental data from Gurven and Walker, 2006) above and beyond her own maintenance requirements. Thus, given the astounding amounts of energy involved in human reproduction and offspring rearing, differences between archaic and modern humans in reproductive and growth parameters can offer evidence critical to understanding the energetic framework of modern human origins. Faster growth, for example, could be reflected in higher daily energy needs among dependent juveniles, elevating the caloric burden on food providers and increasing the risk of losing offspring due to starvation and disease.

Although interpretations of development in the fossil record are limited by the very small number of available juvenile remains, the data that do exist provide good evidence that a pattern at least resembling that of recent humans has a deep history in the genus *Homo*, meaning that archaic humans similarly had to cope with the energetic demands of long-term nutritionally dependent offspring. The extended human period of growth and dependence likely corresponds to the metabolic demands of growing very large brains (Barrickman et al., 2007; Leigh and Park, 1998; Martin, 1983, 1996, 2007) and the obstetric requirement that they pass through the narrow pelvis of human bipeds (Rosenberg, 1992; Rosenberg and Trevathan, 2002). Skill acquisition and foraging competence also likely play into the slow pace of human development (Gurven et al., 2006). Examinations of pelvic morphology in comparison to neonatal brain size in Neandertals and *H. heidelbergensis* indicate that while the birth process may have differed in character from that of modern humans (Weaver and Hublin, 2009), the timing relative to fetal development was such that childhood and its attendant extension of nutritional dependency was already present in archaic humans by at least 260 ka (Arsuaga et al., 1999; Rak and Arensburg, 1987; Rosenberg et al., 2006; Weaver and Hublin, 2009). Others suggest that the evolutionary interaction between increasing brain size and the maternal pelvis

began much earlier with *H. erectus*, although this was not immediately accompanied by the continuation of fetal rates of brain growth after birth (Simpson et al., 2008; but see Ruff, 2010). In any case, the broad characteristics of substantial brain-related energy needs in infancy and extended development as signified by a period of childhood growth were likely present in both archaic and early anatomically modern humans.

Within the general framework of slowed development in later *Homo* as compared to apes and probably earlier hominins, archaic and modern humans may have differed in the details of the rate and timing of craniodental and postcranial development, with potential implications for age-dependent energy requirements. A considerable body of research suggests that archaic human crania and dentition developed more rapidly after birth than in modern humans. For example, several studies find that the Neandertal pattern of tooth crown and enamel development is ahead of the schedule seen in recent and fossil (including Middle Paleolithic) modern humans (Ramirez Rozzi and Bermúdez de Castro, 2004; Smith et al., 2007, 2010; Thompson and Nelson, 2000), perhaps by 2–3 years (Smith et al., 2007). More rapid dental development appears also to have occurred in *H. heidelbergensis* relative to modern humans (Ramirez Rozzi and Bermúdez de Castro, 2004; Bermúdez de Castro et al., 2003, 2010), although it may fall between the Neandertal and modern human patterns, suggesting that Neandertals and modern humans are derived in opposite directions from their last common ancestor.

There is also evidence for early differentiation in craniofacial traits between modern humans and Neandertals, which may relate to their divergent dental development trajectories. Several studies find that distinctive traits of adult Neandertals and modern human crania emerge very early on, perhaps developing prenatally, and then proceed along different developmental paths (Gunz et al., 2010; Krovitz, 2003; Ponce de León and Zollikofer, 2001; Williams et al., 2002, 2003). Areas of early differentiation include mandibular and midfacial traits, including nasal and palatal breadth and premaxillary suture closure (later in Neandertals than in modern humans; Maureille and Braga, 2002). Cranial vault shape diverges early on as well (Minugh-Purvis, 2002), possibly relating to the pace of attainment of adult brain size, which appears to have proceeded more rapidly in Neandertals than in modern humans. Although both taxa have similar estimated neonatal brain size and appear to reach adult size at the same age, because Neandertals have large average adult brain size this means that they must achieve a larger percentage of adult brain size at any particular age during development (Ponce de León et al., 2008). That interpretation comes from a comparison with recent humans, however, who have smaller average brain size than early anatomically modern humans. Early modern humans had adult brains very similar in size to Neandertals (Henneberg, 1998; Ruff et al., 1997), which would suggest that there was very little difference in the pace of brain growth between archaic and early modern human offspring.

There are other indications that archaic human development did not differ from that of modern humans. Debate has emerged over the implications of enamel development in Neandertal and modern human anterior teeth, with the disagreement centering on whether Neandertal teeth developed more quickly than in modern humans (Ramirez Rozzi and Bermúdez de Castro, 2004; Ramirez Rozzi and Sardi, 2007) or at roughly the same rate (Guatelli-Steinberg et al., 2005, 2007a,b). As noted by Guatelli-Steinberg et al. (2007b), if enamel development is uncoupled from overall somatic growth, it is unlikely to be a reliable indicator of the amount of growth remaining or the somatic/cognitive maturity (and thus foraging capabilities) associated with a particular developmental age in fossil hominins. This presents problems for estimating energy needs on the basis of developmental status as indicated by the dentition. Furthermore, there is some evidence to suggest archaic/modern human parity in somatic growth rates as well. Neandertal postcranial growth falls completely within the range of recent human populations from cold climates and those that experience childhood nutritional stress (Bogin and Rios, 2003; Nelson and Thompson,

2002). Thus, archaic and at least some modern human populations may have shared common developmental experiences and thus potentially similar offspring energetic profiles. In fact, it may be that archaic-modern dissimilarities in dental and facial ontogeny, rather than indicating faster overall growth in archaic human juveniles, instead relate to the development of adult differences in facial anatomy, a topic to which we turn below.

Effects of Energy Throughput Differences on Archaic and Modern Human Anatomy

The above review strongly suggests that archaic humans expended substantially greater amounts of energy, on average, than modern humans. For example, an archaic human male of average mass (78 kg) would have needed to burn roughly 167 kcal/d more than an early modern human male of average mass (67 kg) and 338 kcal/d more than an average recent subsistence-level male (57 kg) simply to meet basal metabolic needs. Differences among females are of a lesser magnitude, although certainly not trivial. To meet basal metabolic needs, an average archaic human female (65 kg) would have needed to burn roughly 86 kcal more per day than an average early modern human female (59 kg) and roughly 209 kcal more per day than an average recent human female (49 kg). The greater energy expenditure among archaic humans would have, in turn, necessitated greater oxygen intake. A liter of oxygen is needed for every 4.8 kcal burned, and thus even at rest an average archaic male would have needed an additional 35–70 L O₂/d relative to his modern human counterparts, while a female would have needed 18–44 L O₂/d more.

When physical activity is taken into account, differences in oxygen requirements are magnified, even if activity levels for the different groups are identical. For example, if a PAL of 2.0 is assumed for all groups, daily oxygen demands would be twice the values presented above, such that an archaic male would have needed to consume roughly 70 more liters of oxygen in a day than an early modern male to burn the calories needed to meet energetic needs. As only 31 mL of oxygen are extracted from every liter of respired air (Schmidt-Nielsen, 1984), this translates to an additional 2,245 L of air per day, or an additional 1.56 L of air per minute. Given that an average adult modern human respire 6–9 L of air per minute at rest (0.5 L per breath at 12–18 breaths per minute), differences in average respiratory demands per minute may not seem that substantial. Daily differences, however, reflect the average of energy expenditure peaks throughout a day, during which oxygen requirements, and thereby respiratory airflow demands, were likely much higher in archaic humans than they were in early modern people. The different respiratory airflow demands were potentially of such a magnitude that they may have been the ultimate cause of some of the primary anatomical differences between archaic and modern humans, namely large thoraces, broad noses, and prognathic faces. To investigate this possibility, we must first address the energy expenditure involved with specific activities that archaic and early modern humans were probably undertaking.

The metabolic equivalent of task (MET) is the ratio of metabolic rate during a specific physical activity to resting metabolic rate obtained during quiet sitting (Ainsworth et al., 2000). Unlike PAL \times BMR, which is the average of an entire day's worth of activities, MET \times BMR approximates the energy expended in the process of a specific task. For example, an activity such as strolling on level ground, which entails very little effort, has a relatively low MET value (2.0), whereas more strenuous activities such as hiking (6.0), jogging (7.0), and running at 9 mph (15.0) have considerably higher MET values. For every 1.0 increase in MET, archaic males would have needed an additional 0.78 liters of air per minute over early modern males. Even at fairly modest activity levels, archaic humans would have required roughly 5.0–5.5 L additional respired air per minute. It is likely that during strenuous activities, archaic humans had

substantially greater respiratory demands than modern humans, and potential inefficiencies in locomotion (see above) may have made the differences even greater.

To meet their elevated respiratory demands, it is possible that archaic humans simply had a faster rate of respiration than modern humans, although this option seems unlikely. As respiratory rate increases, the volume of air per breath tends to decrease (i.e., faster breathing is generally shallower). Of the half-liter of air inspired by the average adult modern human with each breath, only about 350 mL reaches the alveoli and is available for oxygen exchange (the remaining 150 mL is trapped in the respiratory dead space of the tracheobronchial tree, pharynx, nasal passages, and mouth). The volume of air in this space remains the same regardless of depth of inspiration. As a result, deeper breaths at a slower rate are more efficient for oxygen exchange than shallower breaths at a faster rate (Fomon et al., 1950). While breathing deeper is more efficient, however, thoracic size and lung volume places an upper constraint on maximum tidal volume. The oxygen demands of high energy budgets, then, may have favored the voluminous thoraces of Neandertals and other archaic humans (Churchill, 2006; see also Franciscus and Churchill, 2002; Gómez-Olivencia et al., 2009).

Greater ventilatory demands may also be reflected in other aspects of archaic human respiratory morphology. If archaic humans needed greater lung volume to fulfill their oxygen and energetic demands, it follows that the upper respiratory tract—the nasal passages and pharynx—would have needed to enclose a greater volume as well. Narrow upper respiratory tracts would have generated high airflow resistance and greatly increased the work of breathing (see Jelinek, 1994; Franciscus and Churchill, 2002; Yokley et al., 2009). Unfortunately, the nasal aperture, nasal cavity, and roof of the nasopharynx are the only aspects of the respiratory tract formed by bone, and as such, provide the only means we have for assessing the dimensions of the respiratory tracts of fossil humans. Furthermore, while a low degree of basicranial flexion may translate to a deeper nasopharynx, the relationship between the cranial base and adjacent soft-tissue anatomy is extremely complex (Lieberman and McCarthy, 1999; Lieberman et al., 2000). As such, the only direct measures of the dimensions of the upper respiratory tract come from the nasal aperture and skeletal nasal cavity, both of which are broader in archaic humans than in modern humans (Franciscus, 1995; Franciscus and Churchill, 2002). Nasal breadths among archaic humans (both *H. heidelbergensis* and *H. neanderthalensis*) tend to fall in the 30–35 mm range (although the nasal aperture of the African Middle Pleistocene cranium from Bodo measures a whopping 42.5 mm!), whereas the nasal breadths of most early modern humans are substantially smaller, generally falling between 23 and 28 mm (the three Skhül-Qafzeh specimens with measureable nasal breadths are all greater than 30 mm, however, and are a notable exception). Recent humans from cold and/or dry climates have an average nasal breadth of 23.9 mm, whereas recent humans from hot, humid climates have an average nasal breadth of 27.7 mm. The ranges of internal nasal cavity breadths are much more variable, but archaic averages are greater than nearly all modern human groups (Franciscus, 1995).

Among recent humans, individuals from populations that evolved in hot, humid climates tend to have noses that are shorter and broader than individuals from populations that evolved in cold and/or dry climates (Thomson and Buxton, 1923; Davies, 1932; Weiner, 1954; Wolpoff, 1968; Hiernaux and Froment, 1976; Crognier, 1981; Franciscus and Long, 1991). At first glance, Neandertals do not appear to fit this pattern. Neandertals lived in Europe and Southwest Asia during times of glacial advances and retreats, with climates that were, for the most part, colder than they are today (van Andel and Davies, 2003). Their nasal apertures were tall like those found among modern cold-adapted populations, yet much broader, which has led some to downplay the effects of cold climate on Neandertal nasal morphology (Hylander, 1977; Smith, 1983; Trinkaus, 1987a, 1989). However, selection for narrower nasal passages may have been constrained in Neandertals by the respiratory

demands necessitated by their large body mass and high active energy expenditures. While the African *H. heidelbergensis* sample is very limited, the extremely broad nasal aperture of Bodo suggests that the *pattern* of ecogeographic variation in archaic human nasal anatomy may have been similar to that found among recent humans, but that the baseline tropical breadth was much greater due to ventilation requirements.

An archaic-to-modern human reduction in ventilatory demands, related in part to reduced body mass, may have also had direct consequences for the evolution of modern human facial architecture. The extraordinarily broad noses of Neandertals have frequently been explained as the result of plesiomorphic retention of large anterior teeth (Smith, 1983; Rak, 1986), with a correlation between nasal breadth and maxillary intercanine breadth observed in recent human adult samples (Schwalbe, 1887; Glanville, 1969) cited as evidence. Holton and Franciscus (2008), however, recently demonstrated that more variation in nasal breadth is explained through basion-prosthion length (a measure of facial prognathism) than through intercanine breadth. They also observed that, unlike intercanine breadth, the ontogenetic trajectory of basion-prosthion length closely parallels that of nasal breadth. This conclusion is further supported by research on growth at the premaxillary suture (Maureille and Bar, 1999; Maureille and Braga, 2002). Prolonged suture patency is associated with prognathic faces and broader noses, while earlier suture closure is associated with orthognathic faces and narrower noses. The evolution of modern human facial architecture appears to be due largely to a reduction in the growth rate of this region. Reducing growth here may have been the mechanism that allowed modern humans to evolve narrower noses than would have been otherwise possible. If these two traits are truly linked developmentally, the evolution and persistence of orthognathic faces as the predominant form among humans may not have been possible prior to reduction in average body mass. Given the greater oxygen demands of a large and active body and the associated need for voluminous lungs and respiratory tracts, and given the developmental relationship between skeletal nasal breadth and facial prognathism, two of the major diagnostic traits of modern human craniofacial anatomy—narrower noses and orthognathic faces—were probably secondarily related to a Late Pleistocene reduction in human body size (Ruff et al., 1997; Churchill et al., 2012). In other words, a reduction in body size and correspondingly decreased ventilatory demands in modern humans may have relaxed the constraints on naso-facial development that applied to archaic humans.

Energetics and Reproduction: An Anatomically Modern Advantage?

Returning to the premise that biological energy flux serves mainly to fund reproduction, we present a preliminary comparison of the energy requirements of reproductive-age females and their offspring in Neandertals and EUP anatomically modern humans. Recent work has pointed out that differences in energy requirements between Neandertals and early modern humans may have had an impact on fertility rates, possibly explaining the geographic expansion of the latter and simultaneous decline of the former (e.g., Sorensen and Leonard, 2001; Churchill, 2006; Froehle and Churchill, 2009; Snodgrass and Leonard, 2009). To explore reproductive energetic differences between Neandertals and EUP modern humans, we present a modified version of a model for age-specific, daily reproductive caloric demand across the female reproductive lifespan (Gurven and Walker, 2006, including supplemental material). This model estimates the compound daily energy requirements for a mother and all of her nutritionally dependent offspring, from her age at the birth of her first child to her age at the nutritional independence of her last born, which we term “compound age-specific reproductive energy” or CARE.

The model relies heavily on averaged empirical data from recent hunter-gatherers, while recognizing that modern foragers vary greatly in terms of subsistence, reproductive, and social factors (see Kelly, 1995; Panter-Brick et al., 2001); our model is thus admittedly reductionist. In addition, the initial model ignores the common practice of non-maternal provisioning, food sharing, and juvenile contributions to foraging returns among extant hunter-gatherers (Crittenden, 2009; Crittenden et al., 2010, n.d.), which removes much of the CARE burden from mothers. Thus, the model we offer here represents a baseline with which we can assess expected differences in CARE between Neandertals and EUP modern humans using only the energetics-related variables most easily determined from the fossil record: adult body size, juvenile body size growth rates, and cost of transport. From that starting point we can then examine the effects on CARE of likely behavioral differences between Neandertals and early modern humans, as inferred from the fossil and archaeological records, to further evaluate limits to fertility in both groups.

Gurven and Walker (2006) identified four variable sets that contribute to CARE (age-specific fertility, offspring mortality, growth, and foraging capabilities) to which we add a fifth (maternal DEE). We hold fertility and mortality constant for the basic model, to better explore the potential effects of energetic disparities on rates of reproduction. Fertility variables include hunter-gatherer averages (data from Kelly, 1995) for age at first birth (19 years), interbirth interval (3 years), and total fertility rate (six births). We also hold offspring mortality constant at zero as a simplifying assumption, as this likely varied in unknown ways across the fossil groups (see Marlowe, 2005). By holding fertility and mortality constant, we can then predict how they might diverge along with energetic differences between Neandertals and modern humans.

We also use the same modern human averages for birth weight and gestation length (3.4 kg; Dufour and Sauter, 2002; 268 days; Dryoff, 1939, cited in Martin, 2007) for both Neandertals and EUP humans. Both variables correlate closely with neonatal brain size (Martin, 1983, 2007), and Neandertal and modern human neonates appear to share similarly sized brains (Ponce de León et al., 2008). Following Nelson and Thompson (2002), we assume that somatic growth in Neandertals was similar to that of modern Inuit, using age-specific percentages of adult body weight (from data in Auger et al., 1980; Rode, 1984). Meanwhile, the average of tropical forager growth rates from Walker et al. (2006) serves as a proxy for EUP modern human offspring development, since EUP adult body proportions cluster with recent tropical groups (Holliday, 1997). The model assumes that by 18 years of age, both Neandertals and modern humans had reached adult body size (and nutritional maturity; Hrdy, 2005), for which we use group-specific, overall average adult body mass estimates (males, females, and undetermined sex) from Table 8.1. Offspring energy needs are derived from body mass using age- and sex-specific BMR equations (in Henry, 2005) and averaging values for males and females (in effect assuming a 1:1 offspring sex ratio). Again as a simplifying assumption, this basic model holds both childhood activity and food production constant at zero.

Maternal DEE estimates assume energetic parity between Neandertals and EUP modern humans, aside from differences due to body mass and cost of transport (for both of which we use group-specific female averages from Table 8.1). As with offspring, we estimate maternal BMR from body mass using the age- and sex-specific equations of Henry (2005). These equations do not account for potential variation in exposure to thermal stress. Different maternal body mass also likely results in different relative costs of gestation as they relate to maternal tissue gain and maintenance (not including fetus, placental and amniotic fluid—these should relate to neonatal, not maternal, body size)—thus, maternal gestation costs are calculated from maternal body mass, relative to the costs for a 55 kg woman (Dufour and Sauter, 2002). Finally, we estimate maternal average daily thermic

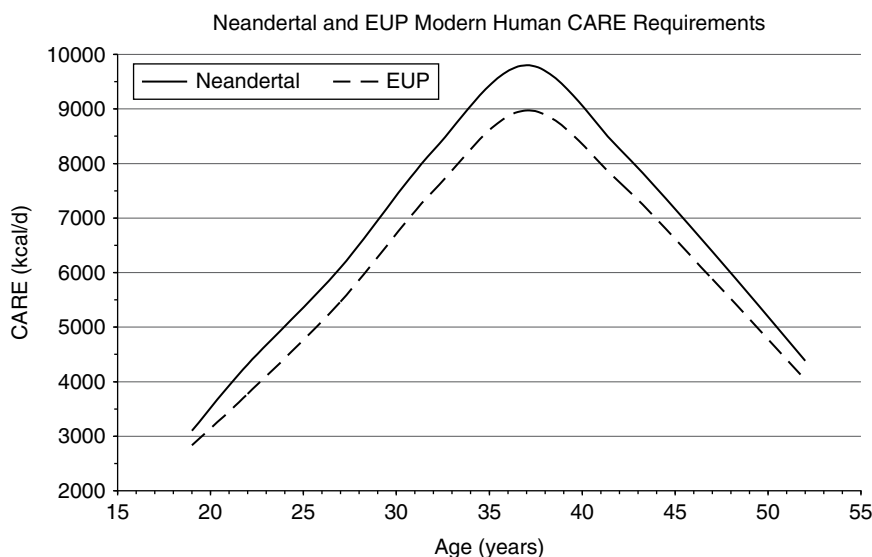


Figure 8.3. Estimates of daily CARE requirements (following Gurven and Walker, 2006) in Neandertals and Early Upper Paleolithic modern humans. Estimates include energy requirements of a single mother and her nutritionally dependent offspring across the reproductive lifespan. All contributing variables are held constant for Neandertals and EUP humans except as related to adult and offspring body size and locomotor costs (see text for details).

effect of food, proportional to BMR, over the course of a year using the mean of summer and winter high-protein diet values from Snodgrass and Leonard (2009). It seems reasonable to assume that both Neandertals and EUP anatomically modern humans would have had diets similarly high in protein, given that they share high nitrogen stable isotope values (Bocherens et al., 2001, 2005; Richards et al., 2001, 2005; Pettitt et al., 2003; Drucker and Bocherens, 2004; Bocherens and Drucker, 2006; Lee-Thorp and Sponheimer, 2006; Richards, 2007, 2009; Bocherens, 2009). Activity costs incorporate day range (9 km, multiplied by taxon-specific average cost of transport) and non-locomotor physical activity level ($1.3 \times$ BMR) data from Ache and Ju'hoansi (!Kung) women in Leonard and Robertson (1997a), which assumes a sexual division of labor where women expend less energy on activity than do men. Finally, we limit our consideration to Neandertals and European EUP early modern humans, as other comparisons suffer from inadequate sample sizes.

When we model average daily energy expenditure for females and their dependent offspring across the reproductive lifespan in this manner, we find substantial differences in energy requirements between Neandertals and EUP modern humans. For each child, average energy cost of gestation and lactation, not including a female's own direct maintenance energy costs, would have been ~ 150 kcal/d higher in Neandertals versus EUP anatomically modern humans. When we include female maintenance requirements, this figure rises to ~ 400 kcal/d. At all ages, a Neandertal female and her offspring would have higher CARE requirements per day than would a modern human female (Figure 8.3). The excess CARE of Neandertals would have surpassed that of modern humans by ~ 250 kcal/d early in a female's reproductive career, rising to ~ 825 kcal/d during the prime reproductive period of 35–39 years old (Figure 8.4). Our model predicts (again, assuming interbirth intervals and fertility equal to the modern human forager averages) that a Neandertal female would enter this interval (at age 35) with six dependent offspring (one infant, two children, one juvenile,

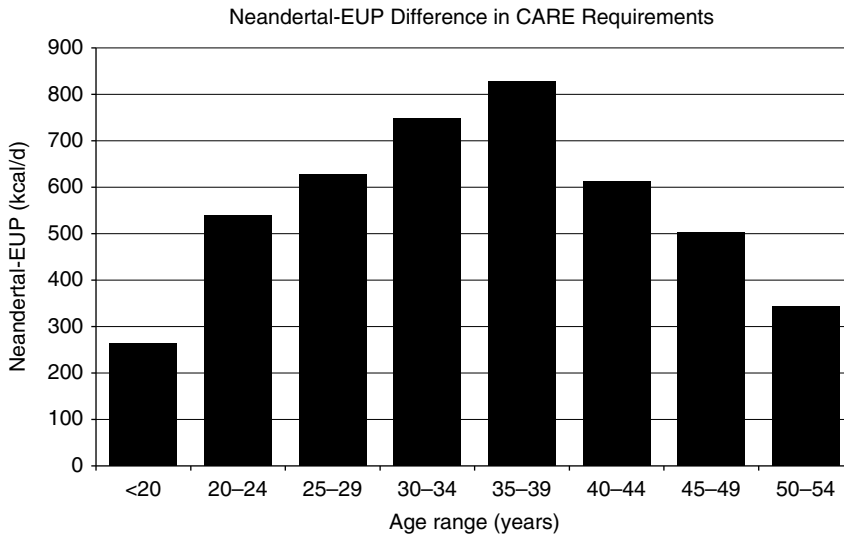


Figure 8.4. Amount by which estimated daily Neandertal CARE requirements exceed those of early Upper Paleolithic modern humans, during specific age ranges across the reproductive lifespan.

and two adolescents, following classification in Gurven and Walker, 2006), requiring nearly 10,000 kcal of daily reproductive investment.

Conservative estimates of Neandertal foraging returns (Sorensen and Leonard, 2001) suggest that, were she providing all of these calories herself, a female Neandertal would have to forage up to ~12.5 hours per day at a PAL of 2.0 (higher than our model's combined locomotor and other activity PAL value of ~1.7) to obtain enough energy during the peak reproductive years. When we consider some of the variables that we held constant in the model, the likely energetic burden on Neandertal mothers becomes even more onerous. For example, less cultural buffering against cold stress may have increased the amount of energy Neandertal adults and offspring alike would have had to consume to maintain body temperature, at least during part of the year (Stegmann et al., 2002; Aiello and Wheeler, 2003). Such a heavy investment of time and energy in foraging would leave no time for childcare or domestic activities, and it is thus likely that Neandertal females relied on provisioning by other productive adults as well as caloric returns from foraging by their older children.

It is also highly likely, however, that Neandertal females were limited to reproducing at a slower rate than modern humans in order to maintain an energy balance favorable to offspring production and survival. Reducing Neandertal total fertility in the model from six to five births, reproductive energy requirements during the peak years drop to a level similar to EUP anatomically modern humans; in the years leading up to the peak, however, Neandertal females still would have required 300–600 kcal/d more than EUP AMH. In terms of demographics, even a 6:5 ratio of modern human to Neandertal total fertility rates could have had profound effects on population size and could have led to the Neandertals' extinction through intensified resource competition within only about 50–60 generations (Zubrow, 1989). Combining reduced fertility with a shift in age at first birth to 20 years old in Neandertals would make their reproductive energy profiles virtually the same as in EUP anatomically modern humans. In populations with high adult mortality (such as the Neandertals; Caspari and Lee, 2004), however, delaying the start of reproduction is likely not a favorable option. Neandertals may have had interbirth intervals as much as 1 year

longer than modern humans, if dental attrition rates provide an accurate picture of the timing of introduction of weaning foods (Pettitt, 2000). While a slower pace of reproduction might reduce age-specific daily reproductive costs, it would also reduce lifetime fertility, especially given potentially high juvenile and young adult mortality rates.

Overall, our model is consistent with previous suggestions that high caloric requirements in Neandertals would have been linked to reduced fertility relative to modern humans (Cartmill and Smith, 2009; Snodgrass and Leonard, 2009). Reduced total fertility is also consistent with evidence for lower population density in Neandertals as compared to early modern humans (Mellars, 1998; Hockett, 2005; Conard, 2006; Kuhn and Stiner, 2006; Mellars and French, 2011), which may also correlate with larger body size in the former (Walker and Hamilton, 2008). In addition, Neandertals may also have suffered higher juvenile mortality than did Upper Paleolithic humans (Soffer, 1992, 1994), perhaps due to caloric stress or micronutrient deficiencies stemming from a meat-heavy diet (Hockett and Haws, 2005), or due to greater juvenile participation in risky hunting behavior (Thompson and Nelson, 2011). They certainly seem to have suffered higher young adult mortality (Trinkaus and Zimmerman, 1982; Berger and Trinkaus, 1995; Pettitt, 2000; Caspari and Lee, 2004), which would have increased the need to begin reproductive careers earlier and to reproduce more rapidly, but this may simply have not been energetically sustainable. Coupled with high juvenile mortality, Neandertals likely had lower fertility than contemporaneous modern humans, which, combined with resource competition from immigrating groups of modern humans, may have fostered their demographic decline during the Late Pleistocene Marine Isotope Stage 3.

Conclusions

The application of bioenergetics to paleoanthropology holds great potential for increasing our understanding of human evolution. With regard to modern human origins, some of the key anatomical traits associated with modernity, such as reduced body size and lower limb morphology, are expected to have had important effects on lowering energy expenditure. In turn, this relaxing of energetic constraints may have influenced craniofacial anatomy by allowing a reduction of the respiratory apparatus. Overall, the pattern of reduction in body size and in naso-facial morphology that distinguishes modern humans from archaic populations is almost certainly associated with a reduction in adult maintenance energy requirements, with potentially major consequences for reproductive success. It seems that such differences would have provided early modern humans who migrated into Europe with a distinct advantage over the existing, larger-bodied Neandertals. A similar scenario may have played out in Asia, too, as migrating modern humans encountered indigenous archaic populations there (e.g., Reich et al., 2010). The question then becomes: what ecological conditions drove the evolution of reduced body size and energy expenditure—and thus the emergence of modern humans—in Africa, while archaic anatomy and energetic profiles remained intact for millennia elsewhere? Continued study of hominin bioenergetics and an expanded understanding of the manner in which anatomy and energetics are linked will help to answer this fundamental question about our origins.

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Chapter 9

Understanding Human Cranial Variation in Light of Modern Human Origins

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The past and present are linked inexorably. It is a given in studies of anthropological genetics and human variation that the patterns of genetic diversity we see in the world today have been shaped by past events, some recent and some ancient. Whether we are investigating the history of human populations and their historic and demographic relationships or the history of specific genotypic and phenotypic traits, we interpret the present in terms of clues regarding what happened in the past. In the past few decades, the related idea that information on current patterns of genetic variation could yield insight into the past has become widely used in studies of modern human origins. Research on the origins of modern humans now relies on considering multiple sources of evidence, including the fossil and archaeological records, ancient DNA, and genetic data from living (or very recent) human populations.

The use of genetic data in examining modern human origins has increased dramatically in the past 25 years. Most of the focus has been on answering some basic questions about the origin of modern humans (Relethford, 2001, 2008). Did modern humans evolve from earlier humans in a worldwide transition, or did they appear initially in Africa and then spread out? If modern humans did appear initially in Africa, then did they replace earlier humans living outside of Africa (such as the Neandertals) or did they assimilate them into their gene pool? A variety of genetic data, including many new DNA markers, have been used to look at these and related questions. The pace of the molecular revolution has led to an ever-changing literature on genetic variation in living humans and its relationship to modern human origins (e.g., Relethford, 2001, 2008; Klein and Takahata, 2002; Jobling et al., 2004; Garrigan and Hammer, 2006; Tishkoff and Gonder, 2007). Genetic analyses have supported the view that modern humans began in Africa and then dispersed through Eurasia, although questions remain regarding the demographic nature of the ancestral African population (whether it is best modeled as a single deme or a structured ancestral population) as well as the possibility of admixture with “archaic” populations outside of Africa, such as Neandertals (Garrigan and Hammer, 2006; Relethford, 2008).

This chapter takes a different approach to reviewing biological variation in our species today. Much of the work in the past 2 decades on global genetic variation has been conducted with an eye toward using this variation to look backward in time to help explain the fossil

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record. Although this continues to be a primary focus, this chapter shifts gears slightly to consider how what we know from the fossil record (both skeletal traits and ancient DNA) tells us about variation in our species today, specifically cranial variation in recent humans. The approach taken here is to look from the past into the present, rather than the present back into the past. Although both approaches are frequently considered in studies of global variation, I suggest that more often the emphasis has been on making inferences about the past. As a long-time student of human variation who found himself involved serendipitously in debates over modern human origins, my primary interests still revolve around present-day variation in *Homo sapiens*. Whereas many paleoanthropologists look to studies of human variation to help understand the fossil record, I seek to use the fossil record to shed light on variation in living and recent human populations. Contemporary human variation is best understood by considering the link between past evolutionary events and the present day, which is ultimately just a snapshot of the ongoing nature of human evolution.

Although this chapter looks at human variation in the broadest sense, my focus here will be on human cranial variation, with less detailed attention to DNA markers and other frequently assessed measures of human variation. My long-term interests have always been in the evolutionary biology of complex traits (Relethford, 2007). Here, I link what we know about modern human origins to what we can observe about cranial variation in recent and living human populations to determine what effect the past has had on the present. Specifically, I seek to answer two basic questions: (1) what is the pattern of cranial variation in living and recent humans? and (2) how has this variation been shaped by the evolutionary and demographic changes that accompanied the origin of anatomically modern humans? This chapter starts with a brief consideration of what I see as the major points of consensus in modern human origins, followed by a brief review of what we know about genetic variation in living humans as it relates to the origin of modern humans. The remainder of the chapter then considers what we know about cranial variation and the extent to which it reflects the same kind of patterns of genetic variation seen in DNA markers that have been shaped during the origin of modern humans.

The Fossil Record: A Starting Point

In order to ask questions about the present in terms of the past, we need to start with a quick review of what I perceive as several points of consensus (or near consensus) about the fossil record. Although I take a somewhat oversimplified view here, other chapters in this book provide the needed depth of detail and consideration of divergent viewpoints. A starting point for this chapter is the African origin of modern humans. Although unambiguous anatomical definitions of modern humans have been questioned (e.g., Wolpoff and Caspari, 1997), there has been increasing consensus regarding a much earlier appearance of anatomically modern humans in Africa than in Eurasia. Some of the key evidence here includes the redating of the Omo 1 skull to as old as 195 ka (McDougall et al., 2005), evidence of early modern humans at Herto in Ethiopia at about 160 ka (White et al., 2003), and dating the Klasies River Mouth site to perhaps 130 ka (Grün et al., 1990). An initial African origin also provides the most parsimonious explanation for the fact that most gene trees appear to have African roots (Garrigan and Hammer, 2006). The fact that not all gene trees have ancient African roots suggests some level of non-African ancestry, perhaps best explained by admixture outside of Africa.

Fossil, archaeological, and genetic evidence suggests an expansion of some modern human populations out of Africa within the past 100,000 years. The appearance of anatomically modern humans at Skhül and Qafzeh 92,000 years ago appears to reflect a limited range

expansion of African moderns, with later expansions throughout Eurasia occurring in the last 60,000 years or so (Klein, 2009). The expansions out of Africa are interesting because other humans lived outside of Africa, which brings up the question of possible interbreeding with these other humans (including those typically labeled as “archaic humans,” a category that often includes Neandertals, *Homo heidelbergensis*, and late-surviving *Homo erectus*). Did interbreeding occur across the Old World, only in some parts, or not at all?

Although patterns of regional continuity have been cited as evidence for gene flow (e.g., Wolpoff et al., 1994; Smith et al., 2005), others have argued against this interpretation (e.g., Lahr, 1996). The case for continuity in Europe is supported by fossil evidence of assimilation of Neandertals into an expanding modern human population in Europe (Smith et al., 2005; Trinkaus, 2007). The appearance of Neandertal characteristics in early modern humans in Europe suggests some then-recent Neandertal ancestry, whereas the absence of many of these traits in living Europeans suggests that the Neandertals became extinct not through replacement but through assimilation with a larger population of moderns in Europe (Smith et al., 2005; Cartmill and Smith, 2009).

The idea of genetic “swamping” through assimilation further suggests a small but non-trivial component of Neandertal ancestry should be present in some living humans. This is exactly what has been found to date with analyses of the Neandertal genome, which estimate between 1% and 4% Neandertal ancestry in living Eurasians (Green et al., 2010). The assimilation of Neandertals in Europe may not be unique. A recent genomic analysis of fossils from Denisova Cave in Siberia suggests that between 4% and 6% of the genome of living Melanesians comes from archaic humans in Asia (Reich et al., 2010). Although many geneticists have previously favored a model of complete replacement, the evidence from ancient DNA is pointing to a more complex model that Bustamante and Henn (2010: 1044) term “replacement plus limited gene flow.” I suggest that this view fits best within the idea of an “Assimilation Model” first favored by Smith et al. (1989) or other ideas of a “mostly out-of-Africa” type of model (Relethford, 2001).

Genetic Variation in Living Humans

Given this rough summary of current views on modern human origins, we can now turn to a consideration of five key observations of genetic variation in living humans and how they reflect our species’ past.

Observation 1: Low Levels of Genetic Variation in Our Species

Our species shows relatively low levels of genetic variation relative to other primate species (Marks, 2010). The level of autosomal genetic diversity that exists in our geographically dispersed species is half that of chimpanzees and gorillas and about a third that of orangutans (Hawks, 2009), all of which are species with a much more restricted geographic distribution. Differences in diversity are perhaps most apparent when considering the “effective” population size of our species. Effective population size refers to the number of reproductive individuals in an idealized population characterized by a set of assumptions including constant population size, equal numbers of males and females, and no population subdivision, among others. Because of deviations from these assumptions in the real world, it is sometimes tricky to associate genetic estimates of effective population size with the actual number of reproductive adults in a population.

Numerous studies have estimated our species’ genetic size to be equivalent to about ten thousand breeding adults (Relethford, 2001; Garrigan and Hammer, 2006; Hawks, 2009).

Although it is tempting to use this number to argue for a small demographic number of adults, we must remember that this is a genetic estimate and may not be an accurate reflection of the actual numbers. For example, Eller et al. (2004) show that under a model of extinction and recolonization of local populations, an effective species size of ten thousand could equate to a demographic reality of several hundred thousand individuals (see also Hawks, 2009).

Reduced genetic variation in our species is most often related to the origin of modern humans by postulating one or more bottlenecks in population size under the reasonable assumption that a reduction in population size results in a reduction in genetic diversity. Given an initial African origin and subsequent dispersion across the Old World, there would have been many opportunities for a population bottleneck to result in the loss of genetic variation due to genetic drift. The problem is that there are a number of possible demographic histories, and fitting all of the molecular data to a specific one has been difficult. Some models argue for an initial bottleneck that resulted from an African speciation event (as opposed to an anagenetic transformation in Africa), and others propose an additional bottleneck resulting from the expansion of some modern human populations out of Africa in the past 100,000 years. Other models have included additional bottlenecks during expansion, such as the entry of modern humans into the New World (Amos and Hoffman, 2010). Genetic analyses of mitochondrial DNA, Y chromosome DNA, and autosomal DNA have given mixed results; there is some consensus on a bottleneck associated with an out-of-Africa dispersion, but not with an initial speciation bottleneck (Garrigan and Hammer, 2006).

Observation 2: Higher Genetic Variation in Africa

The rapid development of DNA markers since the 1980s has led to the discovery that there is more genetic diversity in sub-Saharan Africa than in other geographic regions of the world (Relethford, 2001, 2008; Jobling et al., 2004; Tishkoff and Gonder, 2007). This observation was not seen in earlier genetic studies that relied on red blood cell polymorphisms, most likely because of ascertainment bias where most genetic variants were looked for, and detected, in European samples. The consistent higher levels of DNA diversity in African samples suggest that it is a function of the primarily African origin of our species. Again, multiple demographic histories can affect differences in genetic diversity, which is a function (for neutral markers) of mutation, population size, and elapsed time. Higher levels of African diversity are expected under a model where modern humans existed for many millennia before dispersing out of Africa. The longer a population exists, the more mutations are accumulated, and the higher the level of genetic diversity. Under a model of an out-of-Africa bottleneck, diversity would be initially reduced (because of founder effect) in the non-African populations. A bottleneck also fits the observation that the DNA diversity outside of Africa is most often a subset of the diversity found within Africa (Tishkoff and Gonder, 2007), showing that a number of alleles were lost due to genetic drift during a bottleneck.

Another possibility is that Africa has had a larger effective population size for most of the time span of modern humans, and as such has experienced less genetic drift than smaller populations outside of Africa (Relethford and Harpending, 1994; Relethford and Jorde, 1999). A larger effective population size could simply reflect greater population density and numbers of populations, consistent with ecological and archaeological inference (Eller et al., 2004). Larger effective population size could also reflect demographic history, specifically the effect of bottlenecks. It may be the case that higher African diversity reflects actual population size differences *and* demographic history.

The discussion thus far has focused on higher levels of genetic variation *within* Africa relative to other geographic regions. Africa is also characterized by having higher levels of

among-group variation, the level of genetic differences between populations within a region. We typically measure the amount of genetic variation *among* populations using Wright's F_{ST} or equivalent measure, which expresses the proportion of total variation between populations. Studies of DNA marker diversity typically show higher levels of F_{ST} in Africa than elsewhere (Tishkoff and Gonder, 2007), as well as deeper branches in genetic distance trees. The higher level of population differentiation in Africa could reflect a subdivided ancestral African population characterized by high levels of drift. Models incorporating ancient population substructure in Africa may prove more useful than models assuming a homogeneous African source population (Garrigan and Hammer, 2006).

Observation 3: Genetic Diversity Declines with Distance Out of Africa

The observation of higher levels of genetic diversity in Africa were frequently made using regional aggregates of samples, such as "African," "European," and "East Asian." As more data have been collected for more populations, it has been possible to examine population differences in genetic diversity on a local scale. Such studies have found that the key factor influencing a population's genetic diversity was its distance from East Africa (this center was determined by statistical analysis of the geographic distribution of diversity). The greater the geographic distance away from East Africa (using likely travel distances), the lower the level of genetic diversity (Prugnolle et al., 2005; Ramachandran et al., 2005; DeGiorgio et al., 2009).

One explanation that has been offered for this geographic pattern of diversity is the serial founder model. Here, a small founding population leaves the point of origin (East Africa) and disperses to a new location, experiencing drift and a reduction of diversity because of a bottleneck. Over time, this population grows and a new subgroup splits off to form a new founder population. The repeated sequence of founding events with subsequent drift will lead to a linear decline in genetic diversity from the point of origin, which is precisely the pattern seen in human DNA markers (Ramachandran et al., 2005). This simple model, however, may not be realistic because it ignores migration between neighboring groups, which seems unlikely for human populations. However, DeGiorgio et al. (2009) have found that a modified serial founder model that allows migration between neighboring populations also fits the observed data. Further, they also find that limited admixture with "archaic" human populations would also produce the observed decline in diversity out of Africa (this would not be the case for long-term persistent mixture between archaics and moderns). As is typical in much of modern human origins research, alternative models can provide the same fit to observed data, requiring additional research and insight to distinguish between them (Relethford, 2001). Given that it seems unlikely to posit total isolation between neighboring groups for a long time, and given the evidence for limited admixture with archaic humans from ancient DNA, I suggest that DeGiorgio et al.'s serial founder model with migration and admixture is a better description of model human origins than the basic serial founder drift model.

Observation 4: Low Levels of Differentiation among Geographic Regions

The level of genetic difference between major geographic regions in the human species tends to be low relative to other species (Templeton, 1998). Genetic differentiation is typically measured by F_{ST} , and studies using red blood cell markers and autosomal DNA markers mostly show values of about 0.10 (Relethford, 2002; Madrigal and Barbujani, 2007). This means that roughly 10% of the total genetic variation in the human species occurs between major geographic groups (e.g., Africa, Europe, etc.) and 90% within these groups. Measures of

differentiation such as F_{ST} are affected by mutation rate, effective population size, migration rate, and elapsed time. In terms of modern human origins, the relatively low global F_{ST} value could reflect insufficient time since groups dispersed out of Africa to reach a (higher expected) equilibrium and/or the propensity for human groups to migrate, both locally and over long distances. More research into the dynamics of population expansion will be needed to attempt to distinguish between possible causes.

Observation 5: A Strong Global Correlation between Genetics and Geography

When we look at the genetic differences in neutral genes among human populations across the world, geographic proximity is the single major factor explaining these differences. Quite simply, human populations tend to be most similar to their neighbors than to populations farther away (recent migrant groups are of course an exception—the generalization offered here applies best to indigenous groups). The close relationship between genetics and geography has been seen in many studies (e.g., Imazumi et al., 1973; Cavalli-Sforza et al., 1994; Eller, 1999; Relethford, 2004b; Manica et al., 2005; Ramachandran et al., 2005; Romero et al., 2009).

It is important to note that the best way to examine the relationship between genetics and geography is to use likely travel distance rather than a straight-line distance in cases where the latter is unlikely. A good example here would be geographic distances from the Old World to the New World. Straight-line distances connecting populations in Africa, Europe, and Asia to the New World would cut across either the Atlantic or Pacific Oceans, a route not supported by archaeology. Instead, geographic distances from the Old World to the New World should be constrained via “waypoints” that connect the hemispheres in Siberia, thus representing the route most likely traveled in the peopling of the New World. Waypoints are often used to provide approximations of entry/exit points in Northeast Africa, Southeast Asia, and Northeast Asia (e.g., Relethford, 2004b). Thus, the measurement of geographic distance is constrained by population history.

This strong relationship of genetics and (adjusted) geography can be explained by two phenomena. First, individuals tend to find mates close to home, which means that there will be on average more migration with a neighboring group than with a distant group. Second, genetic affinity with a neighboring population reflects common ancestry and history. As human populations expanded out of Africa, each group would necessarily have a closer genetic affinity with the parental group than a population more distant in time and space. A question remains concerning the relative importance of local migration and isolation by distance versus a geographic gradient resulting from serial founding (Relethford, 2004b; Ramachandran et al., 2005). As with the diversity cline, the geographic-genetics correlation might best be explained by a serial founder model with migration and limited admixture (DeGiorgio et al., 2009).

Implications for the Study of Human Cranial Variation

I have attempted to relate what we know about modern human origins to both the fossil record and five general observations regarding genetic variation in our species. The question now turns to considering what relevance this information has for our understanding of cranial variation in living and recent *Homo sapiens*. If we accept the fact that our species' genetic variation has been shaped by key events in the origin of modern humans, such as the initial appearance of modern human anatomy in Africa followed by dispersion with admixture, then should we see the same types of patterns in cranial variation in our species today? (Note that the same question could be asked of dental variation or some other form of quantitative trait, but the discussion here is restricted to cranial variation.)

The answer to this question relates to long-standing debates in both science and popular culture regarding “nature” versus “nurture.” To what extent does a complex trait, such as a measure of cranial size or shape, reflect genetic or non-genetic influences? Historically, there are countless examples of arguments being made from one side or the other, ranging from full-blown hereditarianism to full-blown environmentalism. In anthropology, one good example of continued debate has been the reanalysis of cranial data collected by Franz Boas on American immigrants from Europe (Sparks and Jantz, 2002; Gravlee et al., 2003). Boas had originally analyzed these data and found that there was an environmental influence on head shape relating to whether the children of immigrants were born in Europe or the United States. My own work suggested that both sides of the debate were correct in certain contexts, depending on the questions asked. My own view is that Boas *was* right in that changes in environment did lead to changes in cranial shape, but even then, there were patterns of population affinity that persisted. In other words, cranial plasticity obscured, but did not erase, population history (Relethford, 2004a).

Such debates have relevance to the evolutionary analysis of cranial variation. To what extent does cranial variation in living and recent humans reflect the genetic history of our species described by DNA variation? Although cranial traits are to some extent heritable, do environmental and developmental influences obliterate any past signature of our history? In terms of genetic influences, do the genes underlying cranial variation reflect the neutral (or near-neutral) model used in much molecular research, or has natural selection had an effect? If so, then did selection obscure or erase population history? A final question is to consider the relevance of such studies for studying the *fossil* record. When we study cranial (or other traits) in the fossil record, are we seeing the evolutionary history of our species, or has that been overwritten by selection as well as non-genetic influences? The answer to these questions is important not only to the analysis of cranial variation in living humans; it also has relevance for those who study cranial variation in the fossil record with an eye toward investigating population affinity.

Patterns of Cranial Variation in Living (and Recent) Human Populations

I now turn to each of the five observations on genetic variation in living humans outlined earlier to see if they can be tested using craniometric data, and the results of such analysis. Although these observations can be examined using traditional statistical methods, greater insight has been provided using analytic methods derived from models of quantitative population genetics (Rogers and Harpending, 1983; Williams-Blangero and Blangero, 1989; Relethford and Blangero, 1990). A number of recent studies (as will be reviewed below) have shown that global craniometric variation on average fits a neutral model of population genetics (see also reviews by Roseman and Weaver [2007] and von Cramon-Taubadel and Weaver [2009]). In short, the history of modern human origins has shaped our craniometric variation in much the same way as it has shaped our DNA variation.

Levels of Variation in Our Species

Given the results of DNA marker studies, we would predict that living humans would also show restricted cranial variation relative to other species. To the best of my knowledge, there has been no systematic analysis of cranial variation across primate species that relates directly to the types of DNA marker studies cited earlier. However, some research supports the hypothesis of limited cranial variation in living and recent humans. Howells (1989)

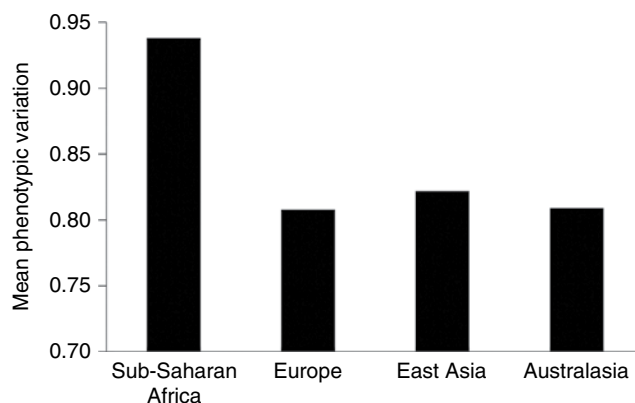


Figure 9.1. Phenotypic variation based on craniometric traits in four geographic regions. This figure shows that craniometric diversity follows the same pattern as seen in DNA markers—diversity is greatest within sub-Saharan Africa. Following Relethford and Blangero (1990), mean phenotypic variation was taken as the average variation across traits after conversion to Z-scores. These figures are based on analysis of fifty-seven craniometric traits as described by Relethford and Harpending (1994).

collected fifty-seven cranial measurements on skulls from twenty-eight male and twenty-six female samples across the world, which has provided one of the single best datasets for looking at cranial variation in recent human populations (and which has been used by many of the craniometric studies reported below). In one set of analyses, he looked at principal component scores using these groups as well as three archaic human skulls (Broken Hill, La Chapelle, and La Ferrassie) and nineteen additional crania of earlier modern humans, mostly from the late Pleistocene. The prehistoric crania were quite different in both size and shape, and Howells suggested that modern humanity is limited in cranial variation (1989: 71). Schillaci (2008) has also found a tight clustering of modern human populations relative to earlier modern and archaic samples.

Higher Phenotypic Variation in Africa

Given that DNA markers consistently show higher levels of variation in Africa, we expect higher levels of cranial variation in Africa under a model where phenotypic variation mirrors neutral genetic variation. Relethford and Harpending (1994) used Howells's craniometric data to demonstrate that phenotypic variation was greater in sub-Saharan Africa than in other geographic regions, in agreement with the expectations of a neutral model (see Figure 9.1). Similar results have also been demonstrated by von Cramon-Taubadel and Lycett (2008) using Howells' data after size-adjustment and by Manica et al. (2007) and Betti et al. (2009) on a different dataset.

Henry Harpending and I (Relethford and Harpending, 1994) also considered past population dynamics as a factor in explaining regional differences in diversity. Using a model that relates among-group and within-group variation, we found that the observed phenotypic variation in sub-Saharan Africa fit a model of larger effective population size in Africa (similar results were also found using this model for DNA markers—see Relethford and Jorde [1999]). Although the data fit a simple model of regional differences in population size, this does not mean that the actual population history is best explained by a simple model of constant population size where Africa is and always has been larger. Indeed, given

the fossil and DNA evidence, this seems unlikely. However, it is important to remember that regional differences in effective population size can be explained by a number of different demographic histories with bottlenecks of different size and duration. As noted above, debate continues about the best demographic model for explaining genetic variation in living humans. The important point here from the craniometric analyses is that the *same pattern* of regional differences in variation applies and most likely reflects the same population history. It is also interesting that the pattern of higher phenotypic variance in sub-Saharan Africa has also been found for dental metrics (Hanihara and Ishida, 2005) and skin color (Relethford, 2000).

DNA marker data also show that genetic variation outside of Africa is a subset of variation within Africa (Tishkoff and Gonder, 2007), consistent with a bottleneck associated with an out-of-Africa dispersion. At present, the hypothesis of a reduced set of alleles outside of Africa cannot be tested from craniometric data because our observations are phenotypic traits and not genotypes. However, advances in identifying the loci underlying phenotypic traits, such as Quantitative Trait Loci analysis (Rogers et al., 1999), could someday allow comparison of allele distributions.

Phenotypic Variation in Relation to Distance from Africa

Genetic studies show a clear decline in DNA diversity with increasing distance from eastern Africa consistent with some form of a serial founder model. Under a neutral model, it is expected that craniometric variation will show the same pattern. Several studies have confirmed this prediction with different global datasets (Manica et al., 2007; von Cramon-Taubadel and Lycett, 2008; Betti et al., 2009). There appears to be little impact of climate (and possible selection) on the out-of-Africa gradient. Betti et al. (2009) found almost no impact, and von Cramon-Taubadel and Lycett (2008) found only a slight effect relating to inclusion of high latitude populations. Overall, the decline in genetic diversity from East Africa is mirrored in craniometric variation.

Low Levels of Phenotypic Differentiation

Williams-Blangero and Blangero (1989) and Relethford and Blangero (1990) developed a multivariate method for estimating Wright's F_{ST} measure from quantitative traits. I later applied these methods to the Howells craniometric dataset to estimate the level of differentiation among major geographic regions (Relethford, 1994, 2002). Using a reasonable estimate of average heritability, global F_{ST} values ranged from 0.11 to 0.15 depending on choice of geographic regions used in the analysis. These estimates are roughly equivalent to regional F_{ST} values derived from blood polymorphisms and autosomal DNA markers, most of which range from about 0.10 to 0.12.

The above analyses used all fifty-seven of Howells's craniometric traits, thus giving an average value of differentiation. Although this is the appropriate choice when comparing F_{ST} to genetic-based estimates derived from large number of loci, an average can also mask some important differences among groups of craniometric variables. To assess this, Roseman and Weaver (2004) used principal components analysis of size-adjusted measures to examine different dimensions of shape-related craniometric variation. They found that estimated F_{ST} was higher for some measures, particularly those involving the nasal region. This analysis shows that some patterns of interregional craniometric variation are still likely affected by natural selection, and choice of variables may be critical in some contexts. These studies show that variable choice can have an impact on how clearly population history can be revealed in craniometric analysis.

The Correlation of Craniometric Distance with Genetic and Geographic Distance

As several studies have shown a strong correlation between genetic distance and geographic distance reflecting an African origin and dispersion and local isolation by distance, we would expect the same results to apply to craniometric distances under a neutral model. More specifically, we expect a strong global correlation between genetic distances and craniometric distances. When genetic data are not available for comparison with some populations, geographic distance can be used as a proxy for genetic distance because of the strong correlation between genetics and geography (Betti et al., 2010; Relethford, 2010).

Several studies have demonstrated a strong correlation between genetic and craniometric distances on a global level. Roseman (2004) examined this relationship by comparing craniometric distances using the Howells dataset with genetic distances based on DNA markers from Rosenberg et al.'s (2002) dataset. Although the exact same populations were not represented in both datasets, he found ten populations that were geographically and/or linguistically similar to the populations in the Howells dataset. Overall, there was a strong correlation between genetics and craniometrics (0.49). Roseman also found that there was a strong correlation with a distance matrix of temperature differences, suggesting some influence of natural selection to climate. Closer inspection showed this correlation was primarily due to the inclusion of a Siberian population (Buriat) in the Howells data. Roseman also found that some measurements showed a greater relationship with climate than others did, most notably cranial breadth, cranial size, and nasal height. Several other studies have also shown a strong correspondence of genetics and craniometrics, as well as finding that some measurements provide a stronger signal of population affinity than others do (e.g., Harvati and Weaver, 2006, 2008; Smith, 2009; von Cramon-Taubadel, 2009a,b).

Other studies have tested the hypothesis of neutral variation in craniometric variation by looking at the correlation between geographic distance (constrained through waypoints) and craniometric distance between human populations. These studies use geographic distance as a proxy for genetic distance because of the demonstrated high correlation between geography and genetics. By using geographic distance as a proxy measure of expected population affinity under a neutral model, more samples can be analyzed because of the relatively small number of samples for which both genetic and craniometric data are available. An example of the correlation between craniometric distance and geographic distance on a global scale is shown in Figure 9.2, based on a multivariate analysis of samples from twenty-six populations around the world (see also Relethford, 2004a).

Comparison of craniometric and geographic distances has provided additional insight by further comparison with genetic and environmental data. I found a strong global correlation between geographic distance and craniometric variation that was found in analyses of both red blood cell polymorphisms and DNA markers (Relethford, 2004b), providing further confirmation that, on average, craniometric distances follow patterns of neutral genetic markers even though the former have been affected, to some extent, by natural selection. In another analysis of the craniometric distances (Relethford, 2004a), I found significant correlations between craniometric distance and both geographic distance and temperature distance, the latter suggesting that populations in different climates have diverged to some extent because of natural selection. However, statistical adjustment for climatic variation did not affect the pattern of relationship between geographic and craniometric distance to any major extent, suggesting that even though natural selection has affected cranial traits, this selection has not erased population history.

Betti et al. (2010) performed a similar set of analyses using a different (and larger) craniometric dataset and found a higher correlation of craniometric distance with geography than with

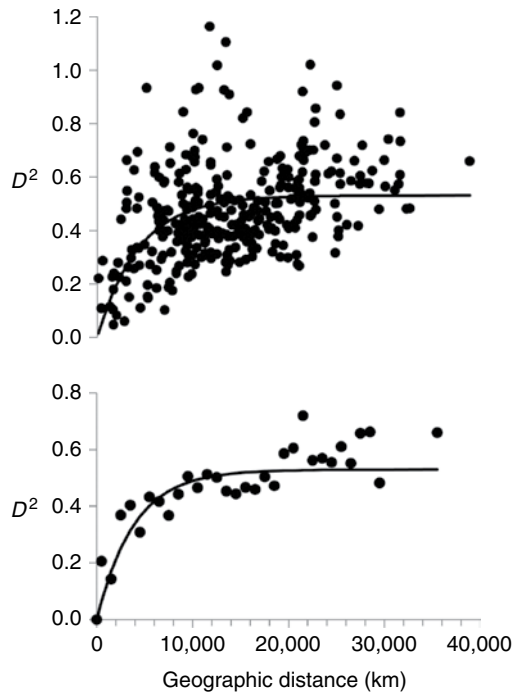


Figure 9.2. Relationship between the squared genetic distance (D^2) estimated from craniometric variation and geographic distance (d) among twenty-six human populations from the Howells craniometric database, as described by Relethford (2004a). The top graph shows the distances between each pair of populations, and the bottom graph shows the average distances within 1,000-kilometer distance intervals. By averaging within geographic distance groups, the general pattern of relationship between genetic distance and geographic distance is easier to see. The genetic distances were estimated using an average heritability of 0.55, but the choice of heritability only affects the scale of the distances and not the relative relationships between populations. The solid line indicates the fit of the theoretical relationship between D^2 and d according to the isolation by distance model: $D^2 = a(1 - e^{-bd})$. For the bottom curve, the non-linear regression line was computed weighting each point by the number of cases within each geographic distance interval.

temperature, suggesting that natural selection has had less impact on global craniometric variation than population history. As with Roseman's (2004) analysis, much of the association with climate was due to the inclusion of populations from very cold climates (those with a minimum annual temperature less than -20° Celsius). The traits that showed the greatest impact of climate were breadths and nasal measures.

As these studies have shown that populations from extremely cold climates tend to deviate from the expected neutral model, I recently took a different approach designed to focus on identifying outlier populations (Relethford, 2010). Here, multidimensional scaling plots were derived from both global geographic and craniometric distance matrices and Procrustes rotation was used to compare the pattern of craniometric variation among twenty-two populations to the expected patterns from neutrality based on geographic distances. Overall, the two distance measures agreed with one another, but there were three noticeable outliers. Two of these were populations that were more craniometrically distinct than expected based on their geographic location—the Buriat of Siberia and the Greenland Inuit. Both populations are from very cold climates, suggesting that natural selection had acted to make these groups more

different than expected under a neutral model. A third population, Peru, was also an outlier, but in this case, the population was more similar to other Native American populations in North America than expected from its geographic location in South America. This outlier might be because the New World was populated relatively recently (in evolutionary time), and since human populations had spread into South America rather quickly, there has been insufficient time for these populations to have reached an equilibrium expected to correspond with a larger geographic distance. Interestingly, the same deviations were also seen in an analysis of red blood cell polymorphisms (although not with DNA markers, perhaps because of a higher mutation rate causing equilibrium to be reached more quickly).

Implications for Human Evolution

As noted by Roseman and Weaver (2007), many past studies of cranial variation in human evolution have tended to focus on adaptationist explanations stressing the role of natural selection or developmental explanations stressing anatomical function. According to Roseman and Weaver, what have typically been ignored are evolutionary explanations that explain cranial variation in terms of population history resulting from genetic drift and gene flow. The idea that morphological variation is less precise at untangling population relationships goes back to the birth of anthropological genetics, where the benefits of studying blood types were lauded over analysis of metric traits (Boyd, 1950). Over the next few decades, new technologies gave way to numerous red (and white) blood cell polymorphisms becoming state of the art, which in turn were largely replaced by the host of new DNA markers available since the late 1980s. Given this history, it is not a surprise that research on craniometrics and other metric traits seems archaic to many (Relethford, 2007). Indeed, I recall mentioning my research on cranial variation to a non-anthropologist and then being asked, “Isn’t that nineteenth century?”

The past decade has seen a resurgence in studies of metric traits in studies of human variation and evolution (Relethford, 2007; Roseman and Weaver, 2007; von Cramon-Taubadel and Weaver, 2009). The results of such work, some of which has been reviewed in this chapter, shows that craniometric traits can and do provide us with a useful tool for analyzing population structure and history. The molecular revolution has helped lead to this reassessment by providing data from which to derive expectations under a neutral model. This does not mean that craniometric variation is entirely neutral or that natural selection and developmental processes have no influence. Far from it. The point is that although such influences can sometimes obscure underlying population history, they do not erase it. As shown in this chapter, we are still able to see the genetic signatures of human variation produced by our species’ history of an African origin and dispersion. Although deviations from a neutral model occur (most notably size-related variation in extremely cold climates), the *overall* pattern of craniometric variation is remarkably similar to that seen in DNA markers: higher variation in Africa, an out-of-Africa gradient in within-group variation, and a close correspondence of among-group variation and geography constrained by known migration routes.

This is not to dismiss the obvious advantages of DNA markers over craniometric traits. However, on the same hand, the advances in DNA technology should not take away from our appreciation of the wealth of information that we can learn from studying cranial variation. The battles of past decades over whether one should use genetics *or* anatomy to reconstruct population history are no longer appropriate. *Both* sources of data tell us something about evolutionary past and present. This new view on cranial variation is best described by the title of Roseman and Weaver’s (2007) review paper, which shows that this is not an either/or situation—“Molecules versus Morphology? Not for the Human Cranium.”

The lesson that cranial variation provides us the same picture of our species' history as do DNA markers should also reassure paleoanthropologists who analyze cranial measures of our ancestors. Although it might have at one time been tempting to ignore such studies, the studies of cranial variation in living humans discussed in this chapter provide justification for looking for clues about phylogeny and population relationships from measuring fossil skulls. An emphasis on cladistic analysis does not mean that metric analyses have no place in our research—see Stringer (1994) for a good example of how these different approaches complement one another.

The usefulness of cranial studies of fossil hominins can be increased by using results from studies of living and recent humans as a guide for choice of methods and measures. Already there has been considerable progress in using comparative studies of genetic and cranial variation to determine what parts of the human cranium are more likely to show phylogenetic signals (Roseman, 2004; Roseman and Weaver, 2004; Harvati and Weaver, 2006, 2008; Smith, 2009; von Cramon-Taubadel, 2009a,b). Of course, we also need to keep in mind the obvious problems with the fossil record in terms of lack of completeness of individual specimens, generally small sample size, and a frequent need to pool data from different times. Some of the more elaborate methods that are used in studies of living human populations, such as ways to estimate migration matrices from metric traits (e.g., Blangero, 1990), are probably never going to be able to be applied to the fossil record because of sample size issues. Nonetheless, we are reaching a state where both methodology and available data can be used to test hypotheses of human evolution. A good example here is the study of Neandertal craniometrics by Weaver et al. (2007). Whereas cranial differences between Neandertals and modern humans have often been discussed in terms of climatic adaptation, biomechanical differences relating to the use of front teeth, and different linguistic abilities, Weaver et al. showed that the null hypothesis of genetic drift could not be rejected. In other words, “Neandertal and modern human crania may simply represent two outcomes from a vast space of random evolutionary possibilities” (Weaver et al., 2007: 135). According to Ackermann and Cheverud (2004), genetic drift may have had a greater effect than natural selection on cranial differences throughout the evolution of the genus *Homo*.

Although the emphasis in this chapter is on the ways in which the fossil record (including ancient DNA) can inform us regarding the recent evolution and global variation of modern humans, it should also be clear that insights from studying the present can also be used to make inferences regarding the past (e.g., Ackermann and Cheverud, 2004; Weaver et al., 2007). To date, much of the emphasis has been on how the genetic evidence from living humans supports an African origin of modern humans (leaving aside for the moment the debate over admixture outside of Africa). Although this inference is important, I suggest that a more significant aspect is the degree to which evidence from *both* the fossil record and the genetic structure of modern humanity has been converging on this finding. Much of the genetic data can have multiple interpretations (Relethford, 2001) and, by itself, the case for an African origin would be weaker. The congruence of evidence from fossils and genetics on modern human origins, much like the congruence of fossil and genetic evidence for the question of the ape/hominin split, presents an opportunity for these two different windows on the past to supplement each other.

Together, the genetic evidence and the fossil record (which now includes ancient DNA) are beginning to paint a picture of a more complex pattern for the evolution of modern *Homo sapiens*. What have we learned? The modern humans origins debate has often centered around two issues: (1) did modern humans appear first in Africa or more gradually over time across the Old World, and (2) did modern humans interbreed with earlier human populations, or were they effectively a separate species incapable of sharing genes? (Relethford, 2001, 2008). Given the data to date from fossil, genetic, and archaeological

evidence, I argue that the first question has been answered and that modern humans appeared first in Africa, significantly earlier than elsewhere, and then dispersed throughout the Old World (although not all at once—there appears to be an early dispersal into the Middle East). The big question that remains is the degree of interbreeding with earlier non-African populations. Some past answers to this question have tended to be all or nothing—either gene flow was relatively commonplace and persistent throughout much of our species' past, or modern humans were a reproductively isolated species with *no* interbreeding possible.

Although the fossil record shows examples of regional continuity that suggest at least some interbreeding, the most significant insights have come in the last few years with the genomes of both Neandertals and Denisovans. These studies show that there has been a limited amount of interbreeding on a local level in at least two places and times. For example, the Neandertal genome may point to a brief period of contact and interbreeding between Neandertals and modern humans in the Middle East, and the Denisovan genome suggests some interbreeding with an “archaic” human population somewhere in eastern Asia. Local episodes of interbreeding have to be considered alongside the likely frequent extinction of local populations in the past and their effect on genetic variation and evolution (Eller et al., 2004; Hawks, 2009). Local populations can become extinct but their genes can persist over time if there was an episode of gene flow that occurred before they became extinct. The Neandertal and Denisovan genomes suggest this type of event—these populations no longer exist, yet some of their genes remain in some human populations today as the result of interbreeding. Imagine now that this has happened not twice but perhaps dozens or hundreds of times over the millennia, and the “origin” of modern humans now becomes a complex mosaic of “origins” that is the sum of many events, some global, some regional, and some local. To solve this type of problem, the integration of data and models from paleontology, genetics, and archaeology is critical. We need this multidisciplinary approach as we move our focus from global to regional to local.

With this challenge in mind, I view the most significant event of the past several decades as the increasing collaboration and cooperation between those of us that study the living and those that study the dead. The student of human evolution and variation will need increased exposure and training across what has become the truly multidisciplinary discipline of paleoanthropology. The paleontologist will need to study molecular and population genetics, and the geneticist will need to study skeletal anatomy and the fossil record. My advice to the next generation is to read outside of your subspecialty and to attend different sessions at conferences. Explore the common interests and questions and avoid arguing about which data are “best.”

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Chapter 10

The Relevance of Archaic Genomes to Modern Human Origins

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Nearly seven billion people inhabit our planet. At least six billion carry the genes of Neandertal ancestors. Inheritance from Neandertals makes up approximately 3% of the genomes of randomly chosen people outside sub-Saharan Africa today (Green et al., 2010; Reich et al., 2010). A back-of-the-envelope calculation shows if we took all of the Neandertal genes from today's human population, we would have enough raw material to make up 180 million Neandertals.

Before these recent genetic findings, some paleoanthropologists had admitted the possibility that Neandertals contributed some genes to later populations but argued that such mixture was so slight as to be evolutionarily insignificant (Stringer, 2002). But the sheer amount of Neandertal contribution casts their evolutionary importance in quite a different light. We can surmise that a fraction of neutral genetic variation in all living people outside Africa comes from this population. This fraction is well over the amount necessary to guarantee the persistence of any Neandertal variants that are adaptive in the context of later populations (Hawks and Cochran, 2006).

A smaller number of living people, maybe as few as thirty million in island Southeast Asia and the Pacific, carry a genetic heritage from a second ancient population, represented by the skeletal material from Denisova Cave, Russia (Reich et al., 2010). The whole-genome data from one Denisova skeletal individual show a significant contrast from the available genome data from Neandertals, demonstrating at a genetic level the substantial geographic structure within the metapopulation of Pleistocene Eurasia. This genetic structure contributed disproportionately to different regional populations outside Africa today in a multiregional pattern.

The genomes of these archaic humans, coupled with information from large samples of living humans, bring us new ways to investigate the process of modern human origins. Neandertal genes that survive in living people can provide a “tracer” of ancient population movements and founder effects. As we consider these genomes, we find new interpretations for the pattern of variation in living people. Some simple hypotheses about the origin of modern humans can now be eliminated, allowing us to examine more complex

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models. Here we give an account of some of the ways that genetic data have changed our understanding of modern human origins in the last few years.

In this contribution, we review some ways that this information from ancient genomes now alters our view of modern human origins. The study of Neandertal and Denisovan genomes is just beginning, but already the results clarify some long-standing problems in paleoanthropology. For example, the retention of genes from Neandertals in much of the world makes it clear that the human population did not undergo a single massive bottleneck within any single geographic location. We can use the genetic variation retained from Neandertals as a way to trace later movements and population contacts. A more complex scenario of modern human origins requires us to revisit the mechanisms by which the phenotypic variation in recent people must have originated. Today, humans have very few amino acid changes that are fixed in the present population and absent from Neandertals. This means that the variation of archaic people can still be found in our present population, and that our current phenotypic variation draws upon the ancient genetic variation to some extent. Probably, phenotypes have evolved by “soft sweeps” in frequency, or by changes in the regulation of genes, rather than the complete substitution of new mutations.

Bottlenecks and Founder Effects in Late Pleistocene Humans

Haigh and Maynard Smith (1972) were the first to hypothesize that the present genetic variation could be explained by an ancient population size bottleneck in our ancestors. They did so on the basis of a simple calculation of predicted variation under a given population size. Genetic variation refers to the number and frequencies of alleles in a population for a given gene locus. The generation of new alleles by mutation increases variation. The loss of alleles by genetic drift decreases variation. Natural selection against deleterious alleles will decrease variation, but balancing selection may retain variation in the population. Thus, the genetic variation is the consequence of these different historical processes. Haigh and Maynard Smith (1972) emphasized the effect of random genetic drift in a small population as an explanation for the present genetic variation in humans.

A Wright-Fisher population model (e.g., Fisher, 1930; Wright, 1931, reviewed in Hawks, 2008) assumes that a population mates randomly with no selection and is described by one parameter: the number of individuals, which is constant. Assuming this model, genetic drift becomes a very simple process that generates a linear relationship between genetic variation and the population size. When we measure the genetic variation in a natural population (for instance, by tabulating allele frequencies), the “effective population size” is the number of individuals in a Wright-Fisher model that would give rise to the same expected genetic variation as in the observed natural population. The effective population size refers strictly to the assumptions of the Wright-Fisher model. We can explain the failure of ecological data on population size to match the effective population size in terms of failure of the model’s assumptions.

Haigh and Maynard Smith (1972) showed that polymorphism of the beta-globin protein sequence in living people is *too little to be consistent* with a Wright-Fisher model with the large population size of recent humans. They *therefore* hypothesized that an ancient population bottleneck—a many-fold reduction in numbers for some period of time in the past—would explain the low present variation. By the mid-1980s, many others had reached similar conclusions from different genetic systems, including protein polymorphisms from across the genome (Nei and Graur, 1984) and mtDNA restriction fragment polymorphisms (Brown, 1980). The estimate of human effective population size derived by Haigh and Maynard Smith (1972), around ten thousand individuals, would apply to most sets of genetic data studied within the last 30 years.

Over time, it became clear that this value could not be explained by a short population size bottleneck but instead must have required a prolonged period of high inbreeding lasting hundreds of thousands of years. Cann and colleagues (1987) noted that either a severe, very short bottleneck or a long, shallow one would have similar effects and did not resolve the two. Later scholars noted that neither the protein polymorphism data nor nuclear DNA polymorphism data could be explained by a short bottleneck. Instead, a bottleneck lasting at least the last million years of human evolution would be necessary (Li and Sadler, 1991; Takahata, 1993; Harpending et al., 1998). Fay and Wu (1999) determined that some kind of short, severe bottleneck (on the order of 1,500 generations) might resolve the discrepancy between signatures of population growth observed in mtDNA and the lack of such evidence in nuclear DNA at that time (Harpending and Rogers, 2000). Later assessments of nuclear genetic variation increased the power of the data to reject a short bottleneck. A long bottleneck scenario appeared inconsistent with the habitation of more than a small part of one continent by our ancestors, meaning that most Pleistocene fossil humans could not be part of the population ancestral to living people (Harpending et al., 1998). Still other geneticists noted that many assumptions of the Wright-Fisher model are violated in humans, meaning that the effective population size may be orders of magnitude smaller than the true number of individuals in population ancestral to humans (Templeton, 1993; Hawks et al., 2000).

Ancient genomes have clarified this problem in two ways. First, Neandertals have even lower genetic variation than living people, showing that recent humans are not a unique case (Reich et al., 2010). More important, the population ancestral to Neandertals and Denisovans, as well as the population ancestral to Neandertals, Denisovans, and Middle Pleistocene Africans, must all have had similarly low genetic variation, based on the comparisons of these genomes (Premo and Hublin, 2009). These comparisons are reinforced by whole-genome evidence from living humans, which shows that genetic variation was limited in the human lineage from the Early Pleistocene, when the effective population size is estimated as approximately 18,500 individuals (Huff et al., 2010). Again, we emphasize that the mere observation of low variation does not itself require a bottleneck, as other possible mechanisms can reduce variation (Hawks, 2008). What is important is that a single Late Pleistocene bottleneck cannot possibly account for the pattern of low variation observed in all these time intervals and across all these spatial subpopulations of Pleistocene people. That is to say, a bottleneck is not sufficient to account for these observations.

Second, a bottleneck affecting all these populations would predict that genetic variation today would be highest in the populations with the highest amount of mixture with ancient groups. To understand why, consider the hypothesis that a bottleneck affected Africans, Neandertals, and Denisovans, independently reducing the genetic variation in all three of these populations at the same time. Many alleles lost by random genetic drift in Africans would persist in Neandertals, and vice versa, merely due to chance. Once these populations came back into contact and mixed with each other, their mixed descendants would inherit the variation from both ancestral populations. The populations with Denisovan mixture would additionally inherit the variation that persisted in that group. For this reason, the living people with the highest magnitude of genetic variation should be the descendants of all three groups, people today who live in Australia, New Guinea, and nearby islands, who today show evidence of Denisovan ancestry (Reich et al., 2011). But what we observe today is the opposite: low variation worldwide, higher within sub-Saharan Africa than elsewhere. This pattern is inconsistent with a structured population that has undergone a recent global bottleneck followed by mixture. The data force us to the conclusion that today's genetic variation emerged within a metapopulation that included the Neandertals, Denisovans, a diverse set of populations within Africa, and *most probably* others.

Ancient Genomes as Tracers of Population History

The Neandertal and Denisovan genomes are more similar to some of the genomes of living people than to others (Green et al., 2010; Reich et al., 2010). This is the crucial piece of evidence that some living humans have Neandertal or Denisovan ancestors. Shared DNA by itself is not sufficient evidence that populations intermixed, because DNA can be shared from the distant common ancestors of two populations. For example, two living people may carry A and B alleles of the *ABO* gene. These two alleles originated approximately 3.5 million years ago in a prehuman population (Calafell et al., 2008). If genetic sequence data were uncovered from *Australopithecus africanus*, it could include the B allele, which would then make it more similar to one of the living humans than the other. But this would not necessarily indicate that one human was a direct descendant of *A. africanus*. Instead, both *A. africanus* and living humans might share the B allele by descent from a more distant common ancestor, an arrangement called “incomplete lineage sorting” (ILS). Ruling out ILS in this case would be possible if we can consider many other genetic loci. ILS is random, so that on expectation any two living humans will share the same fraction of DNA with an ancient specimen. If one shared substantially more genetic material with an ancient specimen than the other, this excess must reflect a disproportionate genealogical connection between the ancient and living individuals. The Neandertal sequences share a substantially higher level of similarity with living humans outside sub-Saharan Africa, indicating that these living populations have close genealogical ties with Neandertals (Green et al., 2010). The same observation is true for the Denisova nuclear genome and present-day people of New Guinea and Melanesia (Reich et al., 2010).

These genealogical connections may be consistent with many different models of population history. As presented by Green and colleagues (2010) and Reich and colleagues (2010), the ancient genomes and living people are embedded within a branching population model with several assumed properties:

1. Living humans derive most (more than 90%) of their ancestry from an ancient African population.
2. This African population diverged from the ancestors of Neandertals and Denisovans at some instant in the past.
3. The African population was isolated from the ancestors of Neandertals and Denisovans after that time.
4. Later, a fraction of the African population began to expand, mixing with Neandertals and Denisovans.

This model in many respects oversimplifies the true population history. Simplification entails a trade-off. By examining a simple model, one may gain the ability to estimate several parameters. For example, Reich et al. (2010) provide estimates for the time of divergence of the sub-Saharan and Neandertal-Denisovan populations (250,000–400,000 years ago) and the time that these populations subsequently mixed (after 100,000 years ago). But the other side of the trade-off is that a simple model must neglect phenomena that may be biologically realistic as applied to Pleistocene people. We are investigating the more detailed pattern of shared genealogical patterns among living and ancient genomes as a way to test the simple population model applied thus far.

For example, populations of the Middle and Late Pleistocene underwent evolutionary changes that are evidenced by the skeletal and dental records. Some of those evolutionary changes involved natural selection. Likewise, natural selection has been abundantly documented in the genetic records of recent human populations, with a rapid increase in new selected

mutations during the last 40,000 years (Hawks et al., 2007). The simplistic population model assumes an absence of selection, so that widespread evidence of selection may cause us to question the resulting estimates. For any single locus, such as mtDNA, natural selection in one or more of the ancient human populations may result in patterns of genetic relationships that are entirely different from those predicted under a population model with no selection (Hawks, 2006). When we consider the entire genome, the pattern of selection is of a different character, because the total number of selected changes must be small relative to the three billion base pairs of the genome. Nevertheless, natural selection acting on human populations of the Middle and Late Pleistocene may have affected the probability of allele sharing among these populations, which would shift the resulting estimates about dates of divergence and mixture. Testing for natural selection in the archaic genomes requires us to identify precisely which genetic regions are shared among them.

The estimates of divergence and mixture time discussed above (from Reich et al., 2010) assume that the origins of Neandertal and Denisovan populations were accompanied by complete reproductive isolation of these populations from contemporary Africans. If we instead explore a population model with a small amount of gene flow among these ancient populations, the “time of divergence” of the sub-Saharan and Neandertal-Denisovan ancestral populations becomes a more complex event involving genetic differentiation within a geographically structured metapopulation. Again, testing the hypothesis of gene flow among these ancient populations requires us to identify precisely which parts of the genome are shared among them. Thus far, the ancient genomes have been compared with living human genomes only at the grossest level of whole-genome similarity. These comparisons are sufficient to demonstrate Neandertal and Denisovan ancestry in some living populations but tell us nothing about which parts of the genome reflect this ancestry. The simple model leaves many interesting questions about the dynamics of Pleistocene people unanswered.

We are interested in the basic question of whether living people have the same Neandertal-derived genes or different ones. The answer to this question can test hypotheses about the pattern of population interaction and movement after our Neandertal ancestors lived. We consider haplotype comparisons for single nucleotide polymorphisms (SNPs) from the international HapMap (International HapMap Consortium, 2005). A finer-scale view of the shared sequence between ancient genomes and many living people can reveal which ancient variants occur today, their frequencies, and whether they are shared or unique to different living populations. This work is ongoing, and Figure 10.1 presents a view of the present population frequencies of Neandertal-derived regions of the genome in living European and Chinese samples for the X chromosome.

The published estimates of human-Neandertal population mixture have been based on comparison of a relatively small number of whole genomes from living people (only five in the initial publication by Green et al., 2010). The resulting estimate of the proportion of Neandertal ancestry in living people outside Africa is a straightforward average across the genome. But given an average of roughly 3% Neandertal ancestry, we might imagine several hypotheses about how that ancestry is distributed. The ancestry might be concentrated in a small fraction of common Neandertal-derived genes, such that most living people share the same few chromosomal regions of Neandertal DNA. In this case, we would find the same Neandertal gene regions no matter which living people we examine. Or, most parts of Neandertal chromosomes might exist today in a few people but are very rare, so that any given person will have only around 3% of them. In this case, examining two living people would discover entirely different genes derived from Neandertals.

In our examination of the HapMap population samples, we find that the second pattern characterizes Neandertal ancestry on the X chromosome. The regions of the X chromosome that people today derive from Neandertals are mostly rare. For most cases in which a living

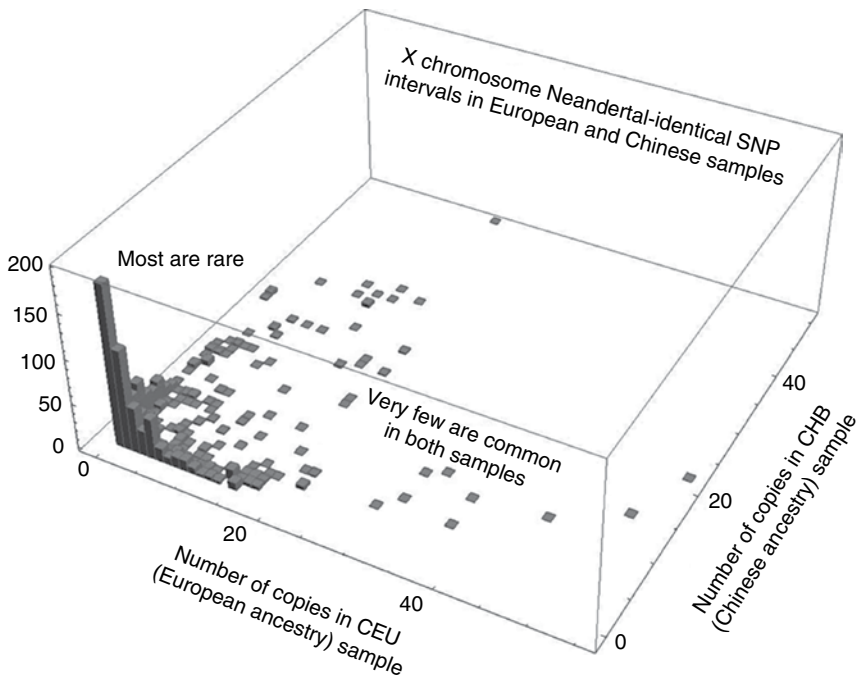


Figure 10.1. Three-dimensional depiction of geographic and frequency distributions of Neandertal-identical X chromosome SNPs in modern Europeans and Chinese. Few Neandertal-identical SNPs are common in both Europeans and Chinese, while many SNPs are restricted to either Europeans or Chinese. Most Neandertal-identical SNPs are rare regardless of population.

member of the sample shares a region of the X chromosome with the Vindija 33.16 genome, that same region is not shared with other members of the sample. The bulk of the variants derived from Neandertals are today at frequencies of less than 1% in this sample.

There are a smaller fraction of chromosome intervals from Vindija 33.16 that are shared with several individuals in the HapMap sample. In other words, the distribution of frequencies of Neandertal-derived alleles has a long tail. A few Neandertal-derived chromosome intervals are at frequencies of 20% or higher today in one or more of the HapMap samples. These loci make up a disproportionate fraction of Neandertal ancestry of a randomly chosen person in the sample, but the majority of that randomly chosen person's Neandertal ancestry is likely unique within the sample or shared with only a handful of individuals.

By comparing HapMap samples with each other, we can examine the geographic pattern of Neandertal ancestry. The initial comparison of whole genomes led to the observation that people outside Africa have approximately the same amount of Neandertal ancestry no matter which region of the world they come from (Green et al., 2010). This leads naturally to the hypothesis that the same Neandertal-derived gene regions are present in all populations outside Africa today. However, our examination of chromosome intervals shared with Neandertals in HapMap populations disproves the hypothesis that different populations have the same Neandertal-derived genes today. Again, this is illustrated in Figure 10.1. The distribution of present frequencies of the Neandertal-derived chromosome intervals shows that most of these are found in only one or two individuals and are therefore not shared among samples. But of the alleles that are common today, in more than one or two individuals in the

sample, most are common only in one geographic region represented by the HapMap. In Figure 10.1, the distribution of frequencies of these variants in Europe (the CEU sample) is compared to the frequencies of the same variants in China (the CHB sample). Only a few Neandertal-derived chromosome intervals are found at frequencies greater than 5% both within Europe and within China. Of those that are common in Europe, most are absent or rare in China. And likewise, those that are common in China are rare or absent in Europe.

This pattern carries information about the pattern of human dispersal within the last 50,000 years. Whole genomes of people outside Africa have approximately the same amount of Neandertal ancestry. Green and colleagues (2010) hypothesized that the mixture of originally African and Neandertal populations had occurred in west Asia before 50,000 years ago, and that subsequently people from this population dispersed elsewhere. This hypothesis might be consistent with any degree of sharing of Neandertal-derived sequences, as long as the overall fraction was approximately the same. But comparison with a larger sample of individuals allows us to refine this hypothesis. The populations that presently occupy Europe and China, for example, have different frequency distributions of variants. This indicates that the populations underwent substantial selection or genetic drift after they acquired a fraction of Neandertal ancestry. Because most of the loci are presently very rare, it is plausible that genetic drift has played a large role in differentiating these populations. If so, the founder effects generated by people who moved from west Asia across south Asia to China, and in the opposite direction into Europe, may have exerted the most important influence on the initial genetic differentiation of those regions. This hypothesis predicts that the actual size of these Late Pleistocene populations was very small relative to contemporary populations within Africa, and compared to their descendants after 30,000 years ago.

MSA Africans and Genetic Diversity

Geneticists have often attempted to identify a point of origin for the dispersal of “modern” humans, as if the emergence *from* Africa were the key event in our evolution. This ignores the process of emergence *within* Africa. Paleoanthropologists have called some Middle Pleistocene fossil remains “anatomically modern,” including the Omo Kibish (McDougall et al., 2005) and Herto (White et al., 2003) remains, despite the great anatomical diversity within the sample of late Middle and early Late Pleistocene Africans (Gunz et al., 2009). Only recently have genetic samples begun to represent the great biological diversity within today’s Africans. The analysis of large samples of African DNA has made it evident that the Middle Stone Age was a time during which African populations had already differentiated into regional groups with restricted gene flow.

Archaeology has extended the emergence of modern human behavioral patterns back to dates that predate the emergence of Neandertals and Denisovans outside Africa. Dated to about 500,000 years ago, blades from the Kapthurin formation of Kenya illustrate that hominins possessed the cognitive and manual skill to manufacture these high-investment, high-risk, and high-reward tools (Rouze-Johnson and McBrearty, 2010). Bar-Yosef and Kuhn (1999) explicitly argued blades are not the exclusive provenance of any one hominin species, nor are blades associated with any singular anatomical feature. Lanceolate blades appear in the Sangoan-Lupemban assemblage of Muguruk, Kenya, which was deposited from approximately 30,000–170,000 years ago (McBrearty, 1988). Biface blades dated to approximately 72,000–77,000 years ago are present in Blombos Cave, South Africa (Henshilwood and Dubreuil, 2011). The Upper Semliki Valley of Zaire preserves a tool industry characterized by its barbed bone points from 90,000 years ago (Yellen et al., 1995). Finally, the Aterian of North Africa (Morocco) features shell beads and pigmentation that

are about 80,000 years old (d'Errico et al., 2009). What unites these traditions is their apparent lack of connection with subsequent assemblages. That is, they are ephemeral, appearing and persisting regionally, with little evidence suggesting they contributed to later material cultures. They suggest but do not prove complex demographics throughout Africa throughout the Middle Stone Age.

Mitochondrial DNA variation within Africa has long been known to show substantial evidence of population structure predating that reflected by mtDNA variation outside Africa. Harpending and colleagues (1993) referred to the “Weak Garden of Eden” model, in which the ancestors of non-Africans emerged from a population that was already substantially structured. Much broader samples of African diversity have reinforced the observation that mtDNA variation in Africa is much more ancient than it is outside Africa. African mtDNA demonstrates regional diversification within Africa as early as 150,000 years ago (Gonder et al., 2007; Behar et al., 2008).

Henn and colleagues (2011) reported on genome-wide SNP data from African hunter-gatherer populations, including Hadza, Sandawe, and San. In conjunction with prior datasets from other parts of Africa, the genome-wide comparisons add substantial evidence about African diversity and population history. African populations extensively mixed with each other during the Holocene, particularly during and after the Bantu expansion (Tishkoff et al., 2009; Scheinfeldt et al., 2010). Even before this, the growth of the Late Stone Age African population, evidenced by autosomal data (Cox et al., 2009), may have driven an increase in migration among African populations. The dispersal of farming across Africa appears to have disproportionately affected the distribution of Y chromosome variation, reflecting a male-biased migration with substantial local survival of mtDNA lineages (Berniell-Lee et al., 2009).

Genetic diversity within African populations remains very high despite substantial Holocene gene flow and mass migration of agriculturalists. Holocene migration and gene flow have reduced the among-population component of genetic variation, so that different African populations today are more similar to each other than would have been true in the past. But this similarity among populations has not reduced the within-population component of variation. The genealogical depth of relationships among individuals within Africa is very deep, reflecting the low inbreeding within the pre-Holocene population. To some extent, present-day hunter-gatherer populations retain a higher level of among-population diversity that would have been characteristic of Pleistocene peoples, but they have not entirely escaped the Holocene pattern of gene flow. Reconstructing the former pattern of higher population diversity yields among-population values that exceed those found among living human populations (Henn et al., 2011).

The pattern of genome-wide variation appears consistent with the mtDNA evidence in favor of substantial differentiation within Africans of the late Middle Pleistocene, 150,000 years ago. We accept this consistency with some caution, as a clear chronology has not yet been derived from the SNP data. Research along these lines is still ongoing. A recent study by Hammer and colleagues (2011) demonstrated that the variation in some sub-Saharan populations may have originated in a structured population that existed well before the MSA, possibly as early as the beginning of the Middle Pleistocene. If these results can be supported by additional data, they imply that the emergence of African regional populations began long before the appearance of Neandertals or Denisovans outside Africa.

We lack a well-established terminology to discuss the interactions of African populations in the late Middle Pleistocene. If we can tentatively accept the results from ancient and modern whole-genome comparisons, we must recognize that non-Africans are closer to some populations within Africa than others within Africa are to each other (Green et al., 2010; Reich et al., 2010). This diversity within Africa is an echo of the late Middle Pleistocene

population structure; living African populations inherited their diversity from a network of ancestral populations that existed long before 100,000 years ago. Additionally, living non-African populations have inherited diversity from archaic populations that lived in Eurasia before 100,000 years ago. The origin of modern humans was an evolutionary process in which the shared phenotypes of recent people emerged within a genetically diverse population across three continents.

What Made Humans Modern?

The “Out-of-Africa” model became influential during the 1980s because it combined genetic and morphological evidence under a single demographic scenario. Specifically, an origin in a single ancestral African population was proposed to explain both the genetic and morphological similarity in recent humans (Stringer and Andrews, 1988). In this event, “modern” humans would simply be the descendants of an initial African population, now including all living people and their immediate ancestors worldwide. Anatomical features shared by living people might be derived from this initial founder population, either by selection or by random chance. Under the Out-of-Africa hypothesis, these “modern” human features are markers of our history but might not have been adaptive.

But paleoanthropologists employed the term “modern humans” long before the specific hypothesis of a Late Pleistocene bottleneck or origin in a single population had been proposed. Generally, the term was employed to describe an anatomical category (for a critique of this usage, see Wolpoff and Caspari, 1996). Some physical anthropologists (e.g., Howells, 1942) accepted anatomical similarity by itself as evidence that “modern humans” had a single recent origin. But anatomical similarity can be explained without positing that recent humans form a genealogical network that excludes all other ancient people. Shared features need not imply genealogical exclusivity.

Now of course we know that the genealogy of recent humans includes Neandertal and Denisovan ancestors. This fact must make us reevaluate the use of the term “modern human” because the members of the group defined by anatomical similarities do not constitute a genealogically exclusive entity. The origin of modern humans happened within geographically dispersed populations of earlier humans. Both demographic and selection processes probably interacted during the process, but it was not a founder effect from a single population.

Ancient DNA evidence gives us some information about this population. There are very few genetic changes near fixation in the worldwide human population that are not also present in Neandertals. Burbano and colleagues (2010) used a targeted microarray method to examine Neandertal DNA for amino acid coding sites where humans and chimpanzees differ from each other. Obtaining the genotypes from Neandertals revealed that humans have only eighty-eight amino acid substitutions that are not present in the draft Neandertal genome. These eighty-eight are not necessarily important to the phenotype. They have not been shown to be concentrated in any particular gene or functional network of genes. The number “eighty-eight” itself is misleadingly precise, because the samples of living human populations that have so far been brought into comparisons with Neandertal genome are very small—numbering only a few hundred individuals in total. This sampling is inadequate to detect rare Neandertal variants that may be present at frequencies lower than 1%. Because of this sampling, we cannot yet conclude that any derived variants absent in Neandertals are actually “fixed” in living people, and eighty-eight must be an overestimate of the number of coding substitutions. Coding substitutions are not the only changes of possible importance to the phenotype, because non-coding substitutions may influence gene expression or regulation, adding to the total number.

The number of human-specific amino acid substitutions is very small, only 0.2% of the total number of amino acid substitutions separating a human from the average chimpanzee. The time spans involved in these comparisons are very different: some 12 million years of evolutionary time between humans and chimpanzees; on the order of 1 million years of evolutionary time between a human and the Neandertal genome. Attributing the human phenotype to a very small number of genetic changes has been a recurring idea in paleo-anthropology. Klein (2000) suggested that modern human behavior was the result of a novel genetic mutation in an African population that gave rise to the out-of-Africa movement of people. Eswaran (2002) instead suggested that a small set of coadapted mutations might interact to produce a modern human phenotype, dispersing together under selection. Knowing that only a small number of substitutions seem to be available, such hypotheses may seem even more tempting. We cannot presently rule out the hypothesis that a relative handful of genetic substitutions may explain what it means to be phenotypically “modern.”

However, there are several reasons why the actual phenotypic evolution of Late Pleistocene people probably involved a more complex set of genetic and epigenetic changes.

Diminishing Returns

Lactase persistence has been under strong directional selection in several parts of Europe, west Asia, and Africa since the advent of dairying (Bersaglieri et al., 2004). Today, the lactase persistence phenotype has a very high occurrence in northern Europe, with fewer than 6% of people having reduced lactase activity as adults (Swallow, 2003). Yet the frequency of the major causal allele is only around 75% today. The dominance effect of the allele means that the phenotype has nearly swept the population rapidly—the allele itself is not present at a detectable frequency in Neolithic Europeans (Burger et al., 2007).

But even after this history of strong selection, the ancestral allele remains in the northern European population at a substantial frequency. Selection against recessive homozygotes becomes less and less effective as the allele approaches fixation, because recessive homozygotes appear as the square of allele frequency. Lactase persistence confers a strong fitness advantage on its carriers and has spread rapidly through the population, but the response to selection is directly proportional to the additive component of variance, which continues to reduce over time. As long as the population continues to grow, and pockets of weaker (or no) selection remain, none of the extant lactase persistence mutations will become fixed substitutions.

This analogy suggests that important phenotypic changes may have occurred within the last 100,000 years without necessarily causing fixed genetic substitutions. Lactase persistence is far from unique; several hundred positively selected variants have rapidly increased in frequency during the past 10,000 years (Voight et al., 2006; Hawks et al., 2007). But very few of these new positively selected mutations have increased beyond a frequency of 70% in any human population. The reasons are similar to those for lactase persistence: as a selected mutation becomes more common, the mean phenotype in the population approaches an optimum. Humans presently have dozens of genetic loci that lighten skin pigmentation in northern latitude populations, and only one of the alleles with this phenotypic effect has exceeded 90% in any living population. Selection on skin pigmentation results in less genetic change as the combined effect of these alleles brings the mean population phenotype closer to the phenotypic optimum. The modern human phenotype may likewise have crystallized within our population as a change in the frequencies of many, many genes. We may predict that few of these genes would be fixed in today's human populations.

Social Ecology and Technology

Social ecology and technology change faster than substitutions can become fixed. Again, we can look to the Holocene evolution of human populations for an analogy to the origin of modern humans. The invention of agriculture induced a series of changes in technology and social ecology. Changes in farming practices, evolution and dispersal of domesticated species, the rise of new diseases, and formation of new social organizations all changed the fitness value of many human phenotypes. Alleles that may have been strongly adaptive in early Holocene populations with early domesticates and diseases may later have lost this advantage, and in some cases would have reverted to lower fitness values, as new domesticates, diseases, and patterns of social organization emerged.

Late Pleistocene humans similarly underwent social and technological changes that were rapid in comparison to earlier humans. Greater raw material transport distances, trade, projectile weapons, food storage, and other aspects of the behavioral patterns of Late Pleistocene people were innovations that impacted social systems and altered the risks and rewards of foraging activity. Such innovations may have required cognitive resources that Middle Pleistocene humans lacked. Late Pleistocene innovations are certainly not arguments *against* the evolution of new cognitive abilities in the people who could adopt them. Still, once these innovations were adopted, they changed the pattern of selection in populations where they were invented or used. Alleles that were directionally selected in populations lacking food storage or projectile weapons may have had different fitness values after these innovations. Archaeological cultures in the Late Pleistocene persisted over thousands of years in populations that maintained different regional patterns of change. The temporal and spatial distribution of these cultures is much smaller than that traversed by an adaptive mutation as it proceeds to fixation. From the mutation's point of view, any mutation that became fixed in Late Pleistocene people must have been advantageous across a very wide array of behavioral and social contexts. But from the population's point of view, any culture would have drawn upon vastly more genetic variants than could ever have become fixed across the diverse human range.

Most of the genetic variants that had any fitness implications would have worked at some times and places but not in others. These would never have become fixed globally, but may nevertheless have contributed substantially to the behavioral evolution of modern humans. A few may have been ephemeral—selected until they were supplanted by cultural innovations. Others may remain segregating in today's population, so that echoes of past behavioral adaptations still remain with us.

Genetic Convergence

Skin pigmentation has been evolving rapidly in Europe and northeast Asia during the last 20,000 years (Sturm, 2009). In both regions, lighter skin phenotypes have been advantageous, and selection has increased the frequencies of many mutations that correlate with lighter pigment in living people. But very few of the alleles that contribute to variance in skin pigmentation today are shared at high frequencies in Europe and East Asia. Each region has a set of alleles that overlaps slightly with the set of alleles that affect pigmentation in the other region. Pigmentation phenotypes have converged in these populations under a similar pattern of selection, but with partially distinct genetic responses (Cheng and Canfield, 2006; Myles et al., 2007). Other polygenic adaptations in recent human populations show the same pattern as pigmentation: multiple alleles in one population, different ones in geographically distant populations. The canonical example is malaria resistance (Livingstone, 1971), and even lactase persistence has a similar pattern

involving multiple mutations that regulate lactase activity in different populations (Ingram et al., 2007; Enattah et al., 2008; Ingram et al., 2009).

It may seem parsimonious to assume that “modern human” phenotypes have a single origin. This assumption is analogous to assuming that light-skinned Europeans and light-skinned Asians must have both emerged from a single light-skinned ancestral population, or that Yoruba, Greeks, and Thais inherited hemoglobinopathies from a single malaria-resistant ancestral population. In the contemporary cases, we reject the apparently parsimonious hypothesis of a single origin because the genetic mechanisms are heterogeneous. Indeed, before the genetic mechanisms underlying pigmentation were understood, anthropologists commonly assumed that light pigmentation really did evolve in a distant ancestral population of non-Africans, possibly the Neandertals. But even without detailed genetic information, each case presents substantial evidence about the phenotype and its ecological setting that help to resolve the recency of the adaptation. The heterogeneity of hair and eye pigmentation, as well as auxiliary pigmentation phenotypes such as olive skin, freckling, and tanning, all argue that European and East Asian pigmentation adaptations differ in their genetic bases, even if we did not have evidence from genetic sequences themselves. The distinctive serological characteristics of abnormal hemoglobins accompany different symptoms and occur in populations where malaria has different histories of endemicity.

Like the Holocene examples, the behavioral patterns of modern humans also indicate that behavioral evolution was heterogeneous and convergent in Pleistocene populations. The clearest sign must be the extensive sharing of behaviors between MSA South Africa and Middle Paleolithic Europeans. European Neandertals made compound tools using heat-processed glues, worked with pigments, collected and produced symbolic artifacts, and occasionally transported raw materials up to hundreds of kilometers. These behaviors are all evidenced at Mousterian sites, where they cannot credibly be explained by contact with non-Neandertals (D’Errico, 2003; Zilhao, 2007). The record within the MSA of southern Africa, including deliberately marked artifacts, decorated eggshell, heat-treated silcrete, and systematic pigment processing, is also heterogeneous with behaviors, often highly localized, appearing and disappearing over time.

What can we say about the evolution of modern human phenotypes? The Holocene record suggests that the evolution of modern humans has involved a much broader set of genes than the few that are fixed today and absent in Neandertals. The behavioral strategies of recent humans emerged within a global population that had strong interregional genetic differentiation, including the Neandertals. This was not a process of singular emergence and diversification; it was emergence in the context of preexisting diversity. Yet demographic expansion of some groups did facilitate the widespread dispersal of many genetic variants. That view accords with the genetic differentiation of MSA Africans, the record of Neandertal and Denisovan ancestry of recent non-Africans, and the role of technical and social changes in the adaptation of Late Pleistocene people.

Conclusion

The modern human origins problem is pre-Darwinian. Samuel Morton (1844) demonstrated that the morphology of ancient Egyptians was present in the oldest Egyptian skeletal samples. For him, this proved the polygenetic ancestry of the races. By Morton’s logic, if races shared a single origin, then people so near the creation should not yet have developed racially typical features. Instead, the races must have been present at the creation.

The antiquity of the races became the central issue underlying the inquiry into modern human origins (Wolpoff and Caspari, 1997). Of course, by the twentieth century, even those

who argued for a recent origin of races (e.g., Howells, 1942) were talking about a much more ancient origin than the Old Kingdom of Egypt. But the fundamental problem was the same: how long did it take for the present racial diversity of humankind to evolve? Howells (1942) argued that recent humans are similar to each other, and different from archaic humans, suggesting a recent common origin for recent humans. Coon (1962) argued instead that the similarities of recent people had emerged by a process of parallelism in distinct populations. Weidenreich (1947) derived common phenotypes from common origins in ancient humans, spread among populations diverse in ancestry by continuous genetic exchanges. Three hypotheses differed along two axes. Were races young and transient (Howells, 1942; Weidenreich, 1947) or old and permanent (Coon, 1962)? And did similar traits reflect identity of populations (Howells, 1942; Coon, 1962) or continual mixture (Weidenreich, 1947)?

Nearly 30 years ago a young researcher observed in the German journal *Das Altertum*, “Wäre es möglich, DNA von altägyptischen Mumien zu isolieren, so ergäben sich daraus fast unbegrenzte Möglichkeiten, die genetische Konstitution der alten ägypter sowie deren Verwandtschaft untereinander und mit modernen ägyptern zu studieren” (Pääbo, 1984). One year later, the first genetic sequence data from a long-dead human were published in *Nature*, 3.4 kilobases of DNA from an ancient Egyptian mummy (Pääbo, 1985). From this recent beginning the study of ancient DNA has brought us Neandertal and Denisova genomes, demonstrating the relationships of these ancient people to each other and their ancestry of living humans.

Now we turn to the mechanism by which our population cast off much of the phenotypic legacy of Middle Pleistocene people despite their ancestry. Again, the fundamental problems concern the plurality or identity of human traits with today’s populations. We cannot yet pose a general answer for this question. The fossil and archaeological records suggest that some of the phenotypic traits typical of modern humans did originate in one place at one time, and others emerged in parallel in many human populations at different times.

The genomes of archaic humans add substantially to this picture. The small number of amino acid substitutions that are fixed in the recent human population testify that phenotypic changes in our recent evolution were not caused by new mutations sweeping to fixation throughout the world. Instead, the genetic process of change was more complex, involving a larger number of genes that changed to a smaller degree in frequency. The emergence of modern humans was a process that unfolded across continents, under a common pattern of selection.

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Chapter 11

The Process of Modern Human Origins: The Evolutionary and Demographic Changes Giving Rise to Modern Humans

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Prologue

Background

The study of human phylogeny has always been contentious; for more than a century after the publication of *The Origin of Species*, reconstructions of human phylogeny often reflected current racial taxonomy (Wolpoff and Caspari, 1997a). Through the end of the nineteenth century and into the twentieth, many paleoanthropologists and paleontologists were evolutionary polygenists who essentially described human races (=subspecies) as having independently evolved from different primate species, some in ancient times and others more recently (Haeckel, 1896; Hooton, 1931; Hill, 1940; Gates, 1948). Later in the twentieth century evolutionary polygenism changed to address the independent evolution of human races (=subspecies) from a single prehuman hominid ancestor (Coon, 1962; Thoma, 1973; Rushton, 1995). Key elements shared by all variations of evolutionary polygenism include the independent evolution of human races (for so long that races acquired their humanity separately) and the tree models at their core. It was assumed that phylogeny explained human variation; the processes that accounted for the separate evolution of species also explained the evolution of “races.”

Even in its heyday evolutionary polygenism was not accepted by all paleoanthropologists (Hrdlička, 1927; Weidenreich, 1928), and after the end of the Second World War as biological races were increasingly rejected by the scientific community, prominent evolutionary schemes could no longer be based on them (at least, not without repercussions). This polarized the developing interpretations of the human fossil record and theories of human evolution. For some, the variation in the human fossil record continued to be interpreted phylogenetically, with taxa now elevated to the species level or above, a viewpoint still prominent among (but not unique to) advocates of the punctuated-equilibria theory (e.g., Groves and Mazak, 1975; Schwartz and Tattersall, 2002). For others, the taxonomy of human variation was reduced to a lower level and the null hypothesis became one of a single

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species lineage, with a reduced number of other species lineages recognized in the human fossil record, and very few, if more than one, in genus *Homo* (at the extreme see Wildman et al., 2003). The predominant single lineage model for *Homo* (Wolpoff et al., 1994) is explained by the hypothesis of Multiregional Evolution (Wolpoff et al., 1984).

Multiregional Evolution

Multiregional Evolution describes the pattern of Pleistocene human evolution¹ as the long-term evolution of central (African) and peripheral populations in a global polytypic species lineage (Wolpoff et al., 1984) that, in recent times, is no longer polytypic (Caspari, 2010; Hunley et al., 2009). This evolutionary pattern is structured by the geographic dispersals of human populations and their continued interconnections through gene flow, population dispersals, and other movements allowing adaptive genes and behaviors, under selection, to spread throughout the human range. The key aspects of the multiregional pattern combine global evolutionary changes under selection as adaptive genes disperse (Hawks and Wolpoff, 2001) with regional continuity; that is, persistence over time of regionally predominant features² in various parts of the world, especially peripheral regions (Wolpoff et al., 1984). Multiregional Evolution, in Templeton's words (2007: 1511), "is not just a single alternative of recent human evolution, but rather is a class of models." Examples of these,³ besides those directly described as "Multiregional Evolution," include the "assimilation model" (Smith et al., 2005), "hybridization with continuity" (Wu, 1998), and "regional continuity (*sensu stricto*)" from Trinkaus (2007).

Multiregional models are structured as networks and not as trees because there is an essential pattern of significant population reticulation at their core (Moore, 1994; Templeton, 1998). The details of reticulation will inevitably be variable; as Templeton (2007: 1511) put it, "population genetic theory and observations indicate that there is a broad range of conditions that will result in this pattern." Thus, multiple multiregional models imply multiple suggestions for how modernity could have arisen. Here we lay out *our* framework for understanding this process.

All of the multiregional models recognize some form of genetic mixture between "archaic" and "modern" populations; in the past, many focused on "how many genes" were mixed, although it is now clear that the important question is actually "which genes?" As we see it, the relevant conditions are set by the probability that the human species was quite small for most of the Pleistocene, totaling as little as one million or less (Eller et al., 2004). Multiregional Evolution explains Pleistocene variation as a consequence of population structure in this small, widespread species, whose populations were intermittently connected in a network of gene flow and population movements. Eller and colleagues suggest it is likely that half or more of the human species lived in Africa, and some estimate the African percentage was even higher (Mele et al., 2011), until the population expansions at the end of the Pleistocene created extensive population growth in other parts of the world. This superimposes the multiregional pattern throughout the human range, with the direction of gene flow across this interconnected network most often from the center of the human range, where there were more people, to the various edges (Wolpoff, 1989a). In the first full formulation of Multiregional Evolution (Wolpoff et al., 1984) a "center and edge" effect (described by Thorne, 1981) was indicated, in which most gene flow went from the African center with its large population to the more sparsely occupied peripheries. Wolpoff and colleagues considered this a persistent pattern throughout the Pleistocene; the continued movement of genes from the center brought new adaptive genes to the peripheries, where regionally predominant features were also maintained, and at no time did African features fully replace the regionally predominant ones. Two elements combine to strengthen the understanding of this pattern: (1) the fact that with more people there would have been more adaptive mutations in Africa, and (2) the evidence for several distinct dispersals out of Africa⁴ (Templeton, 2005; Rasmussen et al., 2011).

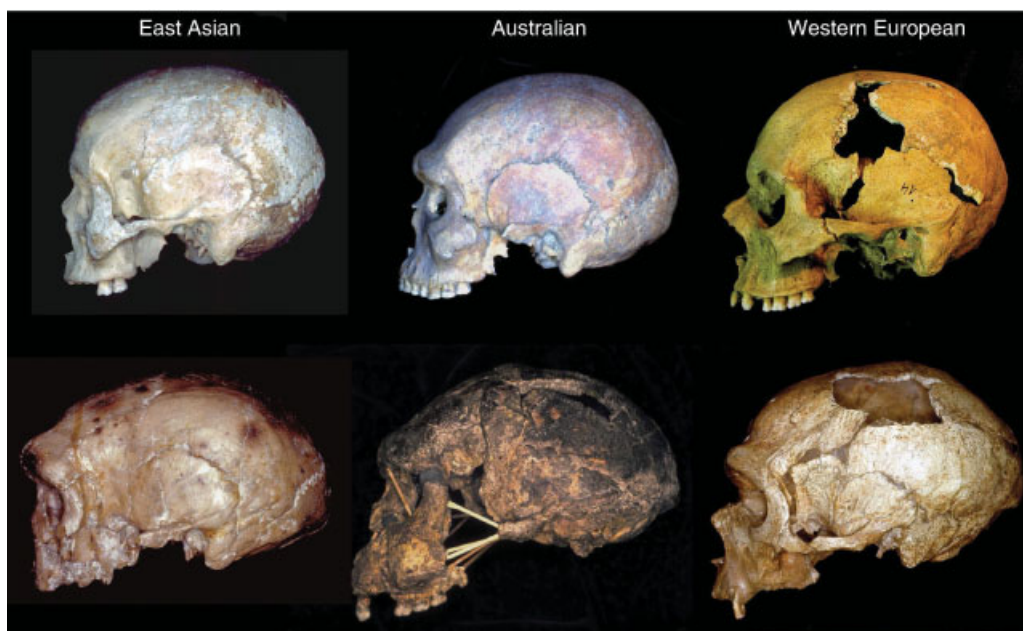


Figure 11.1. Illustration of variation by region and variation over time. Recent (above) and archaic (below) crania from three peripheral regions, far from Africa, oriented the same way to facilitate comparison. The figure illustrates a few broad characteristics associated with the multiregional pattern of evolution. Each set of three crania has features in common that reflect global evolutionary changes between the recent and archaic sets. In general, these are features of vault shape and facial size and robustness. At the same time, the pairs of earlier and later crania from each region have different sets of features in common; for the most part these are facial characteristics, such as nasal angle and zygomatic orientation that differ from one region to the other. The *evidence* supporting the multiregional pattern of evolution illustrated here consists of numerous metric and non-metric characters and their statistical analyses, as detailed in many publications (e.g., Abi-Rached et al., 2011; Frayer, 1992, 1993; Frayer et al., 1993, 2006; Hawks et al., 2000; Skoglund and Jakobsson, 2011; Smith, 1992, 2002; Thorne and Wolpoff, 1992; Weidenreich, 1943; Wolpoff, 1989a; Wolpoff and Caspari, 1997a; Wolpoff and Lee, 2012; Wolpoff et al., 1984, 2001, 2004; Wu, 1998). Many recent crania have features that reflect past regional variation, indicating that *modern variation did not come from a complete replacement of archaic populations by Africans*.

The “center and edge” effect (Hawks, 2011) created different conditions at the peripheries, where gene flow across the network of interconnected populations “can be a strong force that inhibits peripheral populations from evolving to their local ecological optima . . . as a result peripheral populations experience persistent directional selection” (García-Ramos and Kirkpatrick, 1997). For Pleistocene humans, these are regions for which we have paleo-anthropological knowledge, especially certain parts of China, Europe, and Indonesia. This pattern of variation, relating the center and the various edges of humanity, is reflected in the continuity over time of regionally predominant features in these different places (illustrated⁵ in Figure 11.1), that extended beyond the time of initial colonizations (Wolpoff et al., 1984) and through continued Pleistocene dispersals (Templeton, 2007), some continuing to recent or modern times. These continuities involve a number of features but are not the dominant characteristics of genus *Homo*. In all regions the dominant characteristics of genus *Homo* are shared in recent crania, including on average higher, shorter, and rounder vaults with smaller faces and less prominent buttresses. These reflect global changes in the human

species. The persistence of some regionally predominant features does, however, serve to demonstrate that the fossil record, as we know it, does not reflect a complete replacement of local populations by the more numerous Africans in any peripheral region of the world.

It is now evident that the genetic heritage of many distinct regional populations from earlier times was obscured by the significant population expansions and dispersals during the Upper Pleistocene and more recent times (Hawks et al., 2007). One consequence is that today, variation within human populations is greater than variation between them, and while geographic variation exists, it is not phylogenetic; human subspecies (biological races) do not exist (Caspari, 2010; Hunley et al., 2009). Only some manifestations of Pleistocene population structure can be found in recent populations, not because the geographic influence was weak but because the consequences of expanding, mixing populations and increased natural selection were strong.

The key insight of Multiregional Evolution is that evolutionary history and local adaptive variations are related by selection throughout the Pleistocene and account for how genetically interconnected populations in the widespread human species developed and maintained significant geographic differences, while the dispersal of adaptive genes under selection caused global, adaptive evolutionary changes (Thorne and Wolpoff, 1992; Wolpoff et al., 1984; Wolpoff, 1989a; Templeton, 2007). However, toward the end of the Pleistocene this global population structure was increasingly obscured, as dramatic population growth and expansion⁶ with concurrent dispersals and many population extinctions within the Neolithic and later came to characterize the human species.

When Did Humans Become Modern?

How can we describe and account for modernity in this dynamic context? When in the sequence of its evolution did humans become modern? None of our earlier Multiregional Evolution papers fully address these questions, even when they appear in the paper title. We have specifically written on this issue before and concluded that these questions could not be easily answered because anatomical modernity could not be clearly defined (Wolpoff, 1986; Wolpoff and Caspari, 1996, 1997b). We reached this conclusion from our studies that indicated humanity does not have a single recent origin, a fact now recognized by all previous sides of the “origin of modern humans” issue (see discussion below). Our main point in a 1996 paper on modernity (p. 170) was that:

We believe it is probably impossible to arrive at a definition of anatomically modern humans that simultaneously includes the variation of all living people and excludes all members of archaic groups (Wolpoff, 1986; Brown, 1990; Kidder et al., 1992). A populational approach to understanding the place of modern features in archaic populations suggests that even as they appeared, and as they increased in number and frequency, modern features were only part of the normal variation of populations. Were the people who possessed them more modern than their siblings that did not? Of course not. Any meaning of moderns, therefore, must encompass many ancients, and make it seem as though, for long periods of time, archaic and modern people were co-existing, not just on the same continent, or in the same region, but in many cases, within the same family. More important than, and critical to, the issue of how to define modernity, we think, is understanding the evolutionary processes that produced it. Modernity, the way we look at it, was not the appearance of a set of anatomical details, but a process and a pattern of change.

Now, 15 years later, with the current consensus that modern humans are not a new *biological species*⁷ with a *uniquely* African ancestry, we return to these issues of modernity in a multiregional framework. We suggest that modernity cannot be thought of as an

“entity,” and there is no “event” (like a speciation) necessarily linking anatomical, behavioral, and genetic aspects of modernity. In this paper we argue that “modern” in this context is multifaceted and can only be adequately defined as the condition of contemporary humans and their immediate ancestors (also see Stringer, 2012). But more than that, we view modernity itself as a process; here we discuss the anatomical and behavioral characteristics often thought to be “markers” of modernity, genetic aspects of modernity recently ascertained by advances in genomics, and the relationships between these three facets, with a focus on the evolutionary processes that make humans “modern.”

Introduction: What Does Modern Human Actually Mean?

A recent paper by Verna and colleagues discussing some early Aurignacian remains begins with the assertion (2012:605): “it is now evident that ~45–40 ka cal BP saw the final establishment of modern human anatomy across the Old World in all except a few peripheral areas.” Modernity is a concept almost uniquely applied to humans. “After all,” as Tobias (1995: 158) wrote, “we are not in the habit of speaking of ‘anatomically modern elephants’ or ‘anatomically modern hippopotami!’” Even though as Schwartz and Tattersall note (2010:94): “Our species *Homo sapiens* has never received a satisfactory morphological definition”, authors (including those just quoted) continue to propose suites of features or behaviors that are said to uniquely characterize the living species. Often “anatomically modern human” is taken to have a phylogenetic meaning: that *Homo sapiens* is a new, recent, and *modern* species. But this has never been universally believed and “modern human” may be no more than a description of all living people and their immediate ancestors, who differ from earlier archaic *Homo sapiens*. It is invariably unclear exactly how they differ: how far back does modernity go, and who is included in it?

Human modernity can be described in terms of anatomy, behavior, and, we argue, genetics. But if modernity is not phylogenetic, are these necessarily manifestations of the same thing? Does a demonstration of one imply the presence of the others; are they the consequences of the same event? Many have assumed the answers to these questions are positive; we believe this is because they explicitly or implicitly accept the underlying premise that modernity describes a phylogenetic entity that replaced its archaic forbearers and cousins around the world. If true, we could expect that the anatomy, behavior, and genetics of modernity appeared at the same time; conversely, if they were observed together, the simultaneous appearance of these features would provide evidence this new human population was present. But, if modernity is not phylogenetic, there is no a priori reason to expect them to appear together in the human fossil record.

Modern Humans Are Not Simply or Uniquely the Descendants of Recent Africans

It is now widely recognized⁸ that a phylogenetic origin of modernity⁹—that is, the explanation that modern humans are the taxon that descended from the recent appearance of a modern human species of *unique* African origin—is demonstrably incorrect. No matter what species definition is used to describe the diversity of ancient humans—interbreeding human species or interbreeding populations of a single species—the issue of importance to us is whether or not there is a *single recent unique ancestry* for modern populations. There is wide agreement that there was no bottleneck at the origin of modern humans (Sjödén et al., 2012), and modern humans do not have a *single unique ancestry* in a recent African (or any other) population.

The recent finding that significant interbreeding occurred between Neanderthals and modern populations refutes the long-standing model that proposes all living humans trace their ancestry exclusively back to a small African population that expanded and completely replaced archaic human species, without any interbreeding. (d'Errico and Stringer, 2011: 1060)

Paleogenetic evidence now available shows that the evolutionary process resulting in the so-called “early modern” humans in the Upper Pleistocene involved mixture of Africans and others with archaic populations in many geographic regions (Alves et al., 2012). African populations themselves have a record of adaptive introgression¹⁰ from divergent human groups (Hammer et al., 2011; Lachance et al., 2012) and show evidence of gene flow from archaic populations in other regions (Garrigan and Hammer, 2006). These archaic populations providing genes, including Neandertals (Wolpoff and Lee, 2012), were *not* isolated species-lineages.

In the peripheral regions outside of Africa, European Neandertal and Asian Denisovan genes (and no doubt genes from other ancient lines that have not been discovered yet) entered non-African populations, including the descendents of dispersing Africans who encountered them, where they led to adaptive (Abi-Rached et al., 2011) and other changes (Alves et al., 2012; Green et al., 2010; Hawks et al., 2008).

Neandertals and the Denisovan Asians account for some 8% of the ancestry of living non-Africans according to Reich and colleagues (2010), about half that for Neandertals alone, and it has been estimated that 9% of non-African X chromosomes are Neandertal derived (Yotova et al., 2011). These percentages¹¹ are estimates and will no doubt change as more genes and populations are studied, but the estimates are an order of magnitude greater than the percentage of the human population that was Neandertal at any given time. By itself this implies that some of the Neandertal and Denisovan genes were adaptive and increased in frequency under selection after mixture—a fact we can be sure of for a number of genes such as STAST2 (Mendez et al., 2012) and some of the HLA class I system, a vital immune system component (Abi-Rached et al., 2011) whose complex populational origins were described as “multiregional admixture”. The demonstration of diverse archaic contributions to recent and contemporary populations undermines any single origin of modernity model. Without such an explanation, anatomical, behavioral, and genetic concepts of modernity cannot be considered three aspects of the same thing. As we proposed over 15 years ago, it is probably impossible to derive a single meaning of modernity other than that applying to recent and current human populations.

Mixed Ancestry for Moderns

The contention of a mixed ancestry for the earliest modern populations was accepted by many paleoanthropologists before it was demonstrated with paleogenetic evidence. Anatomical comparisons suggested that modern populations had a mixed ancestry (Kennedy, 1992; Kidder et al., 1992; Tobias, 1993, 1995; Zilhão, 2006a). Mixture was the central contention of Weidenreich's polycentric model.¹² We have detailed evidence supporting the interpretation of mixture in many papers authored individually, together, and with others, and have long recognized that the resulting pattern of diversity without race is a key aspect of modernity (reviewed in Caspari, 2010). The *magnitude* of mixture in the ancestry of some early modern populations was addressed in research about a decade ago (Wolpoff et al., 2001) when a hypothesis of dual ancestry was tested in two peripheral areas far from Africa, with well-established fossil records: Australia and Central Europe. Pairwise differences were calculated for a set of non-metric features comparing the best preserved early modern specimen in each region with samples of its two potential ancestors (hence the dual ancestry model): (1) a sample of the earlier specimens from Skhul and Qafzeh in the Levant (adjacent to Africa), and (2) samples of local archaic Neandertals in Central Europe (Figure 11.2) and

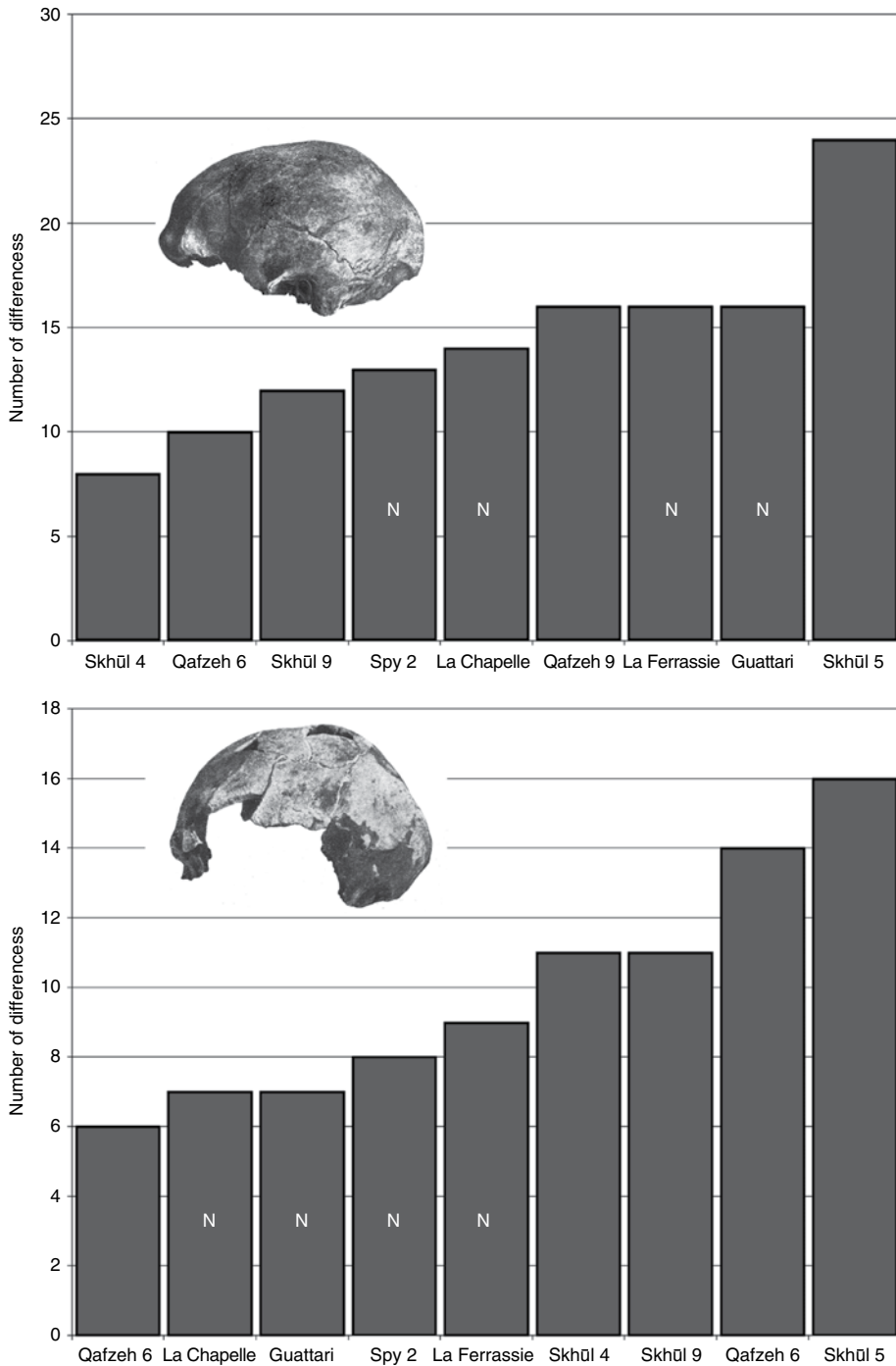


Figure 11.2. In this example pairwise differences between early modern European males Mladeč 5 (above) and 6 (below), are compared with the most complete Neandertal (marked “N”) and Skhul/Qafzeh males. Thirty non-metric traits are used in the Mladeč 5 analysis; twenty-three of these can be observed on Mladeč 6. A sample runs test determined whether the ordering of the number of pairwise differences from the each of the Mladeč crania to Neandertal and Skhul/Qafzeh crania is random (the null hypothesis). Randomness could not be rejected at the $p = .05$ level for either comparison. The Mladeč male vaults are not more similar to Skhul/Qafzeh males than they are to Neandertal males (from Wolpoff et al., 2001).

the Ngandong crania in Australasia. In both cases, the pairwise differences failed to establish a pattern of similarity to only one of the potential ancestors.¹³ Instead, even a low-resolution hypothesis of 50% local archaic and 50% Levantine ancestry for early moderns for these regions could not be disproved (Figure 11.2, and Wolpoff et al., 2001).

Neandertals Are Us, and It Matters¹⁴

Europeans and Australians (and we expect peoples from other regions) did not simply become modern because Africans who were already modern came to Europe and Australia (and other regions) and replaced the local natives; indeed, many of the aspects of modernity that are shared by all human populations evolved after these Late Pleistocene dispersals. We discuss this point further below. This has implications for understanding the behavior of fossil populations. *That the genetic relations of Neandertals and other penecontemporary populations, including Africans, show them to be populations of what could be interpreted as a single biological species exchanging genes has consequences that extend to behavioral capacities.* The genetic exchanges mean that whatever is true of Neandertal cognitive skills, language, social complexity, ability to use and understand symbols, and other intellectual factors, it is unlikely that there were significant differences between their *behavioral potentials* and those of other penecontemporary human populations (Zilhão, 2010b). If behavioral aspects of modernity had a genetic basis, and were advantageous as we would expect, *selection should assure that the genetic basis would disperse everywhere within the network of populations that exchanged genes*, minimizing differences relating to modernity between the penecontemporary populations in it.

This is our explanation for the pattern of shared adaptations in humans today, many of them far more recent than the Late Pleistocene events we are describing. We believe this is the most parsimonious explanation for the universal distribution of any of a number of adaptive genes in the past, such as the FOXP2 “language gene”. Anatomical comparisons show that dispersal of this gene was far more rapid than the dispersal of populations advantaged by having it. No physical traits observable in the fossil record have a pattern of dispersal in time and space that match that proposed for FOXP2. Therefore archaeological evidence for behavioral modernity is unlikely to reflect the dispersal of a single biological population.

Modernity as a Process

All of this recent (and not-so-recent) evidence undermines phylogenetic explanations of modernity and frees us from their constraints. It explains why there never has been an adequate phylogenetic definition of “modern human” (Wolpoff, 1986; Wolpoff and Caspari, 1997b), and why the three aspects of modernity we discuss here are not linked together with their simultaneous appearance at some hypothetical time when modern humans originated.

Modernity has been difficult to define because it does not have a single phylogenetic origin. However, we do not conclude that the anatomical, behavioral, and genetic aspects of modernity are unrelated; on the contrary, we expect *evolutionary processes* to relate them. The question we ask here is “how?” Non-phylogenetic evolutionary processes are related to population structure and its underlying demographic associations. In this paper we discuss a new approach to modernity in terms of its anatomical, behavioral, and now genetic aspects, and propose that all three are related in their common definition as characteristic of all living and recent human populations, and through a unifying process: changes in natural selection and human population history originating as the demographic consequences of increased longevity.

Anatomical Modernity

It was only a few decades ago that “anatomically modern humans” came to be distinguished from “*Homo sapiens*,” as a more recent subset that describes the sole human taxon to inhabit the earth today. During the decade of the 1980s there were various assertions that early modern humans were “instantly recognizable” (Howell, 1984: xxi; Howells, 1981: 74); however, attempts to arrive at a morphological definition of “anatomically modern humans” have been problematic. These attempts began by developing criteria that showed how modern humans differed from Neandertals (Day and Stringer, 1982; Lieberman et al., 2002; Stringer and Andrews, 1988)—in fact, the distinction from Neandertals was the genesis of the “anatomically modern *Homo sapiens* category” (Wolpoff, 1986). Because it was assumed this was a taxonomic distinction with a phylogenetic basis, these attempts were necessarily constrained by the requirement that such a definition should describe most-or-all living humans using criteria that distinguishes them from most-or-all human fossils that are not modern. This requirement was not met, in that the formulations of modernity excluded too many modern humans from Australia, South America, Asia, and Africa (Wolpoff, 1986; Wolpoff and Crummett, 1995). One does not need a smooth brow and a high, rounded forehead to be a modern human being, nor does a thick, continuous supraorbital torus and a low, flat forehead mean that one is not a modern human being.

Recognizing the problems created by defining modern as meaning “not Neandertal,” Trinkaus (2006) took a bottoms-up approach and used a cladistic analysis to ascertain trait polarities. He concluded that early modern humans have more autapomorphies than Neandertals do. But he did *not* conclude that an anatomical definition of modern human (whether early modern or later modern, in his terms) is possible from his findings (p. 614) and his early modern sample (Omo-Kibish, Herto, Qafzeh, and Skhul) is geographically limited to a very small region of northeastern Africa and Western Asia. Without East and Southeast Asian material, it is difficult to interpret his results and even more difficult to disagree with the assessment of Kidder et al. (1992: 175) “that a multivariate study of crania ... [shows] formulating ... a definition of modern *Homo sapiens* is not yet possible, even for European and Near Eastern samples.”

Yet many investigators have continued to use the phrase “anatomically modern,” as though it were based on a known and agreed-upon set of autapomorphies that uniquely characterize all living and recent human beings. Modern humans continue to be described as a “highly distinctive morphological entity” with an “overwhelming gestalt difference” (Tattersall and Schwartz, 2008), even though their unique features characterize only parts of the species and often overlap with other groups that are not “anatomically modern humans”.

Modern Anatomy and African Anatomy

Three areas proved to be problematic in defining or identifying modern anatomy: (1) the anatomy of early modern humans as defined in the literature is not especially similar from place to place; (2) for the most part, early modern human populations have some of the features that are uniquely common in preceding archaic populations from the same region (Figure 11.1); (3) and as we discuss in this section, early modern humans outside of Africa are not uniquely like early modern Africans. Together, this means what paleogenetics has now also shown: *anatomical modernity does not have a single unique African source in a new species that replaces all native populations without mixture*. There is no single source of anatomical modernity and attempts to define a set of modern human features have not failed because of the competence and thoroughness of the investigators, but because there is no such set.

But could we at least stipulate that modern anatomy is principally African anatomy? Africa has played a unique role in the evolution of recent humanity (Caspari, 2007; Smith et al., 2005; Wolpoff and Lee, 2007, 2012), as it has throughout human evolution. Current thinking on the question of an African origin for recent humanity began with a key insight from Protsch (1975); he argued that people resembling recent humans were found in Africa earlier than anywhere else, and therefore “modern humans” must have originated there. While not all of Protsch’s work has held up over the years, this paper has; many, perhaps most, of the dates he proposed have withstood the test of time, and there are new specimens with even earlier dates. This fundamental point was accepted and repeated by some of Protsch’s colleagues; for instance, Bräuer (1978, 1984, 2008), armed with evidence from the dates Protsch published, further argued that Europeans must be of African descent, much as Dart (1940) had proposed earlier.

However, in contending African origins, neither Protsch nor Bräuer insisted that early humans of modern form in Africa implied *unique* African origins. This position first changed with early studies of mtDNA and the African Eve theory, because its insistence that African origin meant *unique* and *exclusive* origin from only Africans—implying a new biological species. Now that the Eve theory is recognizably incorrect, it is reasonable to return to the earlier formulation and ask whether there are unique anatomical features shared by living and recent humans that derive from a shared African descent—did anatomical modernity disperse as Africans dispersed?¹⁵

Armed with today’s knowledge, we may ask whether we can recognize early modern anatomy as African anatomy. In the formulation of the Assimilation Model (Smith et al., 2005: 15), Africa is recognized ...

as the likely source of the basic modern human anatomical form and ... modern humans radiating out of Africa have the major, catalytic effect on the emergence moderns in Europe and Asia. ... the evidence for assimilation stems from anatomical details rather than overall morphological gestalt [for example] of the earliest modern Europeans.

This clearly shows why assimilation is a multiregional model, as we described above, but we believe this formulation remains problematic, as author after author as also described above fails to arrive at a clear and unique description of modern humans that would reflect a common African influence. Moreover, the earliest modern crania from regions away from Africa have no special similarities that are both common to each other and shared with early modern Africans (Figure 11.3). Early modern populations in different parts of the world have African influence through descent; genetic analysis continues to confirm this, and the direction of most Pleistocene gene flow is understood to be from the center to the edges in all multiregional models. But early anatomical and genetic evidence shows modern population variations also reflect local ancestry, and we do not see evidence that their modernity can be ascribed to only one of these sources.

From Europe (Figure 11.4) to Australasia (Figure 11.5), regions farthest from Africa, modern human populations are on average more gracile, the crania smaller and more rounded than their predecessors. One might assume this gracility to be a consequence of genetic influences from Africa, conditions spread by dispersing Africans. But it is not evident that dispersing Africans themselves were especially small or gracile. Gracility does appear early in Africa - 90,000 or more years ago at its Southern tip, but it is not evident that the Klasies folk have any specific ancestry for later dispersing groups. The Herto, Omo-Kibish 2, and Jebel Irhoud specimens are robust, and those fossils thought to represent early modern humans immediately out of Africa, for instance at Skhul in Israel, are not particularly gracile (Figure 11.6). In most regions one source of changes in selection resulting in skeletal gracility came from the consequences of changing technology and organization.

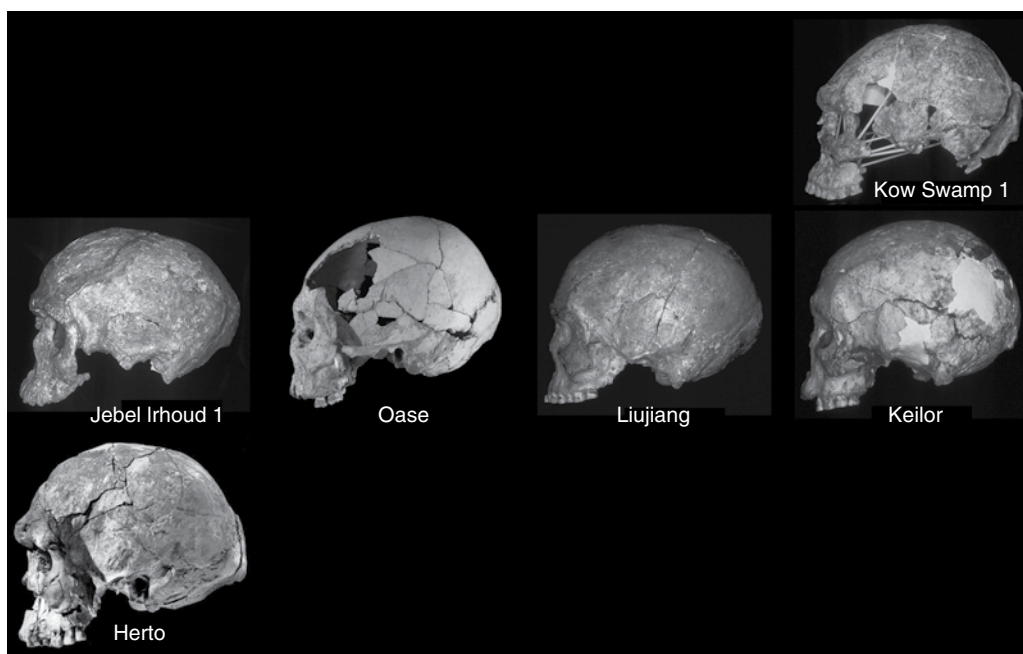


Figure 11.3. Is “modern” the same as “African”? Herto (from White et al., 2003) is the earliest complete modern human cranium from Africa, and Jebel Irhoud 1, almost as complete, is somewhat later. These crania, to the far left, have African features that might be expected to disperse if modernity was an African change. They are shown here with the (later dated) earliest complete or almost-complete modern crania from (left to right) Europe (Peștera cu Oase 2 from Trinkaus, 2010), eastern Asia (Liujiang), and Australia (Kow Swamp 1 and Keilor). These are the earliest specimens with sufficient facial preservation to reflect facial anatomy without the bias that often comes with reconstruction. The question is whether the anatomical features of either Herto or Jebel Irhoud 1 are compelling sources for the shared modern features in the other specimens.

These changes were not the same everywhere, guaranteeing that the details of gracility differed from place to place. Therefore, gracility—potentially the defining characteristic of anatomical modernity—probably does not have a unique African (or any other) source.

Figures 11.1, 11.3, 11.4, and 11.5 illustrate the findings of many studies cited above, that there is local influence of archaic populations on recent and contemporary variation, and that early modern humans in various regions do not particularly resemble the late Pleistocene populations dispersing from Africa. Moreover, our discussion of genetic modernity (below) suggests that many new genes shared by humans today evolved more recently than the Late Pleistocene and some of these more recent genes likely contribute to anatomical modernity. In spite of these shared aspects of modernity promoted by natural selection and dispersed throughout the human species, members of human populations can often be forensically identified (Sauer, 1992).

Is Early Modern Anatomy Modern?

There is a second question about early modern anatomy: is it actually modern? If we use modern to mean similar to living and recent populations, as suggested above, this also is problematic. The very earliest near-modern Africans are the 195 ± 5 kya Omo-Kibish (Day, 1969; Day and Stringer, 1982, 1991; McDougall et al., 2005; Pearson et al., 2008) and the



Figure 11.4. Illustration of regional continuity in Europe. This, and similar figures, are meant to illustrate similarities, not to prove their presence, which is a statistical question for the samples. If the ~35 kya dating is correct for Peștera cu Oase 2 (middle, from Trinkaus, 2010), a specimen found on the floor of a cave, it is described as the oldest modern human cranium from Europe. Its unfused sphenooccipital synchondrosis and the position of the third molars within their crypts show a subadult age at death. It died at an only slightly older age than the late (~40 kya) Neandertal from Le Moustier, the reconstruction shown below from Thompson and Illerhaus (1998). We believe this is an appropriate comparison because the two lived close together in time and there is similarity in dental development and eruption. There are also anatomical similarities that include the cranial shape, cranial details such as occipital bunning, relative size of the mastoid and paramastoid processes, and weak development of the supraorbital tori. The Peștera cu Oase 2 anatomy is exceptionally similar to some recent Central Europeans. It is compared here with the Medieval Hungarian Avar adult cranium 552 from Mosonszentjános (above). All three crania are shown at the same approximate size, in the Frankfurt Horizontal (for Le Moustier the position of the bottom of the orbit is uncertain, and its orientation is matched to the other two by cranial contour). These three crania show general similarities that cannot easily be explained by an overwhelming African influence bringing modernity to the two post-Neandertals.



Figure 11.5. Illustration of regional continuity in Australasia with a comparison of three crania: a recent Australian (top) with face obscured to present the same regions as the other two crania, modified after Weidenreich (1943, Figure 264C); the WLH 50 fossil (cast, middle); and, Ngandong 5 (below) from Weidenreich, 1951 (Plate 23). The specimens are scaled to the same size (in actuality the cranial lengths are 203 mm [Australian], 212.2 mm [WLH 50], and 219.5 mm [Ng 5]). The figure illustrates that modernity is not always the equivalent of gracility. It shows WLH 50 as a credible intermediary between the Ngandong sample and Native Australians. The Pleistocene Australian falls within the Ngandong range. For instance, the occipital plane angle is most like NG 1, the frontal angle is most like NG 10, the frontal flatness is most like NG 5 (shown here). The angular torus and mastoid are most like NG 1. In all of these crania the greatest breadth is at its base, across the supramastoid crests. We contend that these similarities reflect descent (Hawks et al., 2000) and are not homoplasies.

157 ± 3 kya Herto specimens (White et al., 2003). The Omo remains are fragmentary and lack faces (there is a facial reconstruction for Omo 1 but we lack confidence in its accuracy). Herto Bouri remains include a male (BOU-VP-16/1) with a complete face, far better preserved than any of the Omo specimens. The Herto remains were placed in a new subspecies of *Homo sapiens* and described as “on the verge of anatomical modernity but not yet fully modern” by White and colleagues (2003). We accept that BOU-VP-16/1 is a good representative of an



Figure 11.6. The frontal of Skhul 2, a female example of an “early modern human” with decidedly non-modern features, in the sense that they are features not found in recent or living populations. Skhul 2, an *early* “modern female” from just north of Africa, is not in any sense gracile. For instance, the interorbital distance is exceptionally great, and above it the supraorbital torus is thick and continuous across the forehead, projecting strongly from the frontal squama so that there is a deep, strongly expressed supraorbital sulcus.

early African male ancestor of modern humans, and believe there is much to be learned from it because it is not much like the earliest modern males from other regions (Figure 11.3). In their principal components analysis of *Homo erectus*, Neandertals, and modern humans represented in the Howells data set (1989), White and colleagues show a plot of the first two principal component scores places Omo 2 in the Neandertal distribution and Herto between the Neandertal and modern human distributions (p. 741). In an adjacent plot of the first three principal components of the complete Howells data set the Herto adult also lies outside the human range. The authors conclude (p. 741): “this and other results of multivariate analyses demonstrate the phenetic distinctiveness of the Herto hominids relative to modern human crania,” which means the early modern anatomy is not actually modern.

We wonder whether even more recent examples of early modern human remains of African descent are modern, in the sense of being like recent and living populations. For instance, considering Skhul, while there has been much discussion about the affinities of the Skhul males, the less well-preserved females have generally not been the focus of these considerations. We believe they should be and here bring attention to Skhul 2. McCown and Keith (1939) identify this specimen as a 30- to 40-year-old woman, including incomplete cranial and mandibular remains and portions of the forearm long bones. She presents a mixture of features, as all of the Skhul specimens do, but we contend that some of these are unmatched in any recent or living woman from anywhere (Figure 11.6), and like the Herto remains, the Skhul sample might also be described as not fully modern.

The point is that the early modern Africans of the late Middle Pleistocene and early Upper Pleistocene cannot actually be described as modern, and certainly not as gracile. There is little reason to look to this sample for the origin of modern features, especially gracile modern features, seen around the world.

This is not to deny that Africa was a significant source of new genetic variation during human evolution. To the contrary, for most of the Pleistocene the predominant direction of gene flow was from the more densely occupied African center to the more sparsely occupied peripheries of the human range (Templeton, 2007; Wolpoff et al., 1984). The dominance of African population size for most of the Pleistocene has widely discussed consequences (Eller et al., 2004; Relethford, 2003; Hawks and Wolpoff, 2003). One of these is that with

a significant proportion of the world's population for most of the Pleistocene, Africa must also have been a significant source of adaptive mutations. But this does not mean that modernity dispersed with Africans. The earliest of the early modern Africans are not modern in our sense and had many descendents, including some Neandertals (Wolpoff and Lee, 2007, 2012).

The Biological Origin of All Modern Populations Involves Mixture

If it is true that modern populations are not the unique descendents of a recent group of Africans, it is also the case that Neandertals and other archaic populations did not evolve into later Europeans in isolation from the rest of the world and in parallel to it; that would be a polygenic explanation (Wolpoff and Caspari, 1997a). In Europe, where the case against mixture always seemed strongest, there was persistent contrarian evidence, especially from Central European sites, that the earliest modern (post-Neandertal) crania retained a significant number of regionally predominant features that were common in Neandertals and rare in other populations (Freyer, 1992, 1993; Freyer et al., 1993; Freyer and Wolpoff, 2008; Jelinek, 1969; Smith, 1992, 2002; Wolpoff, 1989b; Wolpoff et al., 2001). The earliest modern (post-Neandertal) crania 30,000 years in age and older include: ~35 kya Peștera cu Oase seen in Figures 11.3 and 11.4 (Rougier et al., 2007; Zilhão et al., 2007); ~31 kya Mladeč seen in Figure 11.2 (Freyer et al., 2006; Wolpoff et al., 2006); and ~30 kya Peștera Muierii (Soficaru et al., 2006). There is no single set of Neandertal features in all these crania; different specimens have different features that were common in Neandertals, precisely the pattern found in paleogenetics where most non-Africans have some Neandertal genes that, by and large, appear in different combination from person to person. These anatomical and genetic observations demonstrate that there was early genome-wide intermixture with Neandertals. A significant portion of the intermixture was quite likely in the Levant at the beginning of the Upper Pleistocene (Hodgson et al., 2010), where analysis of the well-published fossil remains from Skhul and Tabun (McCown and Keith, 1939) indicated such a mixture some 70 years ago (Dobzhansky, 1944).

Modernity describes us and our immediate ancestors. Simply put, that description is heavily influenced by the processes of admixture, and so we consider the species-wide pattern of mixture as a key element of modernity. The modern pattern of extensive and persistent mixture is a hallmark of what can be considered genetic modernity (discussed below), a direct consequence of expanding human population size, and much of it came late in human evolution. Perhaps its most significant consequence is that while the human species varies widely and geographically, human variation is not racial or in any sense phylogenetic (Caspari, 2010), another important aspect of human modernity.

All of us have some African ancestry, but Africans alone cannot be the sole, unique ancestors of all. Because of his mixed ancestry President Barack Obama once described himself as “a mutt.” The legacy of modern human origins studies is the recognition that we all are mutts.

Behavioral Modernity

Closely tied to the issues of anatomical modernity are questions of behavioral modernity. Is there a set of modern behaviors that appear abruptly in the archaeological record? What processes account for them? Do they distinguish a modern human behavioral potential from the behavioral potential of earlier hominids as a genetic endowment, or can they be explained

as a consequence of social processes? To what extent can behavioral potentials even be assessed from archaeological remains?

What Is the Archaeological Evidence?

Archaeological discussions of modernity have mainly focused on the issue of what modernity means in the archaeological record (Bar-Yosef and Kuhn, 1999; McBrearty and Brooks, 2000; Wadley, 2001; and many others) and whether modernity appears as a sudden and discontinuous event. The latter has been assumed by many workers, largely because of the Eurocentric focus of much late Pleistocene research and the apparent dichotomy between the Middle and Upper Paleolithic there (Henshilwood and Marean, 2003). More recently, however, evidence has accumulated showing continuity between Middle and Upper Paleolithic assemblages in Africa and Europe (McBrearty and Brooks, 2000; d'Errico, 2003; d'Errico et al., 2001, 2003; Zilhão, 2006b, 2007, 2011). For the most part, however, behavioral modernity is a European construct (Shea, 2011), where Upper Paleolithic assemblages have been thought to reflect modern human behaviors that differed markedly from those of Neandertals, traditionally and mostly associated with the Middle Paleolithic.

The emergence of the Upper Paleolithic is traditionally envisioned in terms of a clear rupture with the Middle Paleolithic. From this perspective, the Aurignacian is interpreted as the culture that would realize the systematization of numerous innovations and become the instrument of victory of Modern Humans over Neandertal populations. (Teyssandier, 2008: 493)

Such discontinuity is said to be found in evidence that uniquely human behaviors such as language, symbols, culture, personal ornamentation, complex society, and higher levels of reasoning all appear suddenly and together. In Europe, initially the source for all models of behavioral modernity, these seemed to appear abruptly in a “human revolution” (Hockett and Ascher, 1964) that was initially thought to accompany the dispersal of modern people into Europe:

Beginning some 35,000 years ago new peoples with new ideas and new designs for living displaced and eventually replaced antecedent Neanderthal peoples and their Mousterian way of life. (Howell, 1969: xxi)

The actual archaeological traits thought to reflect modern human behavioral capacities are varied and combine evidence of technological superiority with what is often considered the emergence of art. The “explosion” of representational and abstract paintings and sculptures that appears in the European record starting about 30,000 years ago is the hallmark of the “human revolution,” symbolic material culture that has been considered evidence of a biologically based human symbolic capacity, uniquely held by modern humans (Mellars, 2005, 2006). Non-symbolic remains are also part of the “package” of modern human behaviors. Henshilwood and Marean (2003, 2006) review features that have been considered evidence of modernity by different authors. Some features, such as the use of non-lithics in tool construction, are not, in themselves, representations of advanced intellect or symbolic capacity; however, because they are thought to reflect an “industry,” their presence, even if isolated, has been considered indicative of modern behavior.

The idea of “modern human behavior” is therefore essentialist in the sense that a very few traits in isolation allow extensive inferences to be made about the whole package, whose essence centers on the abstract and intellectual abilities of the people who made it. These abilities, of course, cannot be directly observed, but they are often surmised, expressed by

the presence of tools systematically formed from non-lithic raw materials (e.g., bone and ivory), the intensive use of blades, increased use of non-local raw materials, and ornamentation. Most important among these are those that seem to represent abstract thought or “style,” non-functional expressions that presumably send social messages. But modern abilities are also inferred from mundane elements, like blades. Implicit in this is the assumption that these artifacts, as a package, actually do reflect a new, modern human intellect, which in turn rises from the hypothesis that behavioral modernity is a distinct entity that is linked to anatomical modernity, having entered Europe in the form of a package of new peoples with new ideas, as Howell (1969) put it. Thus the traditional idea of modern human behavior is closely related to assumptions about the processes that cause it; based on the idea’s Eurocentric origins, modern human behavior has been treated as a biological attribute of modern humans.

A Focus on Processes: Was There a Human Revolution?

There is a long-standing debate over the causes and significance of the so-called “human revolution” in Europe—the “explosion” of expressions of symbolic behavior and complex social relationships manifested in the Upper Paleolithic archeological record (Soffer, 1992, 1994; R. White, 1982, 1989). While some workers see the “human revolution” as cultural change within a species (Clark, 2002; Wolpoff et al., 2004), others believe it represents the biologically based cognitive superiority of modern humans. The problem is, that as traditionally described, anatomical modernity predates behavioral modernity. Some advocates of a biological basis for behavioral modernity (e.g., Klein, 2008) attribute it to a neural change linked to human language some 50,000 years ago that doesn’t manifest itself anatomically; others see it as a latent potential of modern humans.¹⁶ However, these innovations of the Upper Paleolithic can alternatively be understood as a consequence of demographic influence, expanding human populations, without requiring an explanation based on biological changes in cognitive capacity. Moreover, there is considerable debate over whether a human revolution actually exists at all.

Various trait lists defining “modernity” have been critically assessed by Henshilwood and Marean (2003 and in the *Current Anthropology* commentary following). Recently, the very idea of any single trait list signifying modernity has been undermined by the 2000 publication of “The Revolution that Wasn’t: A New Interpretation of the Origin of Modern Human Behaviour” by S. McBrearty and S. A. Brooks. While hold-outs reflecting Howell’s position remain (for instance, Mellars from [at least] 1973 to Mellars and French, 2011, and many others), this shifted much of the discussion to the African continent and emphasized the gradual and seemingly independent African appearances of many of the modern behaviors later found together in the European Upper Paleolithic. These African appearances differed from the European Upper Paleolithic in that they occurred over a much longer period of time and were ephemeral, sporadically appearing and disappearing at different times and places within the Middle Stone Age. Whatever modernity entailed in the archaeological record, it could no longer be considered as a single event.

If the behaviors of the European Upper Paleolithic are not so distinctly different from behaviors of earlier Africans, the other side of the coin is that modern elements have also been identified in the archaeological record of European Neandertals (Caron et al., 2011; d’Errico et al., 2003; Morin and Laroulandie, 2012; Peresani et al., 2011; Roebroeks et al., 2012; Teyssandier, 2008; Zilhão, 2007, 2011; Zilhão et al., 2006) and other archaic Eurasian populations (Hovers and Belfer-Cohen, 2006). In the framework promoted by these and other workers, it is far from clear whether Neandertal archaeology has always been correctly interpreted.¹⁷ Primarily European observations of modern behavioral elements associated

with Neandertals continue to appear in the literature; some show continuity with later Upper Paleolithic industries, others indicate early, unconnected appearances of evidences for modern behavior, often at the same time similar modern behavioral elements appeared in Africa (as in Roebroeks and colleagues' [2012] discovery of an early [200–250 kya] use of red ochre pigmentation). All of this evidence also helps undercut the contention of a “human revolution” accounting for the different behaviors of the Neandertal and Upper Paleolithic peoples in Europe (Zilhão, 2011), a tradition of skepticism embodied in the writings of d’Errico and Zilhão separately (d’Errico, 2003; d’Errico et al., 2001, 2003; Zilhão 2006b, 2007, 2011) and together (Zilhão et al., 2006). Combined with the African data, this indicates that meanings of behavioral modernity are complex and that processes accounting for its appearance are unlikely to be biological.

It is increasingly clear that this is not the modernity of Howells (1969). The attributes associated with modern behavior likely do not have a single origin; as cited above, they appeared ephemerally both in African Middle Stone Age assemblages and in some Neandertal contexts and likely will be found more broadly around the world. Wobst (1976) argues that modernity may *appear* to have dispersed from a single origin, even if it actually emerged gradually in many regions. Wobst’s view is that the *perception* of a single origin and subsequent spread of modernity is a creation of the archaeological record. He demonstrates that the *appearance* of punctuation is inevitable in a model predicated on gradualism: if we assume modernity appeared gradually, we may expect to find what he calls a “cone of modernity” created by viewing the past from the cone’s base in the present. Because of preservation bias, more ancient time slices produce smaller and smaller samples of things that are modern, until there is an earliest. Such a cone would give the illusion that modernity had a single origin in Africa, where there were more people and therefore more evidence of modern traits. But the increasing presence of modern artifacts when approaching the present does not necessarily mean that modernity spread from a single point of origin (its earliest appearance in the record); on the contrary, this would violate the predicated assumption of the model that modernity arose gradually.

Wobst (1977) also discusses social reasons why stylistic changes in (or the attachment of style to) classes of artifacts may appear abruptly once those artifacts become vehicles for social signaling. Many of the features of behavioral modernity may be linked to information exchange within and between groups, conveying broad information to recipients about identity, ownership, authorship, proscription and prescription, religion, and potentially other variables. Intended recipients should be socially distant (so that conversation was not common) but not so remote that they wouldn’t be able to decode the messages. Wobst argues that style, the attachment of such cultural messages to classes of artifacts, will “appear” revolutionary largely because of dangers of miscommunication. Once meaning is attached, style should quickly pervade that class of material culture, and one should expect relative uniformity within a social group; as Wobst argues using examples from mid-twentieth-century Yugoslavia, the dangers of being associated with the wrong social group, or inadvertently sending the wrong message, force rapid conformity of dress (in this case headdresses) within groups. Ultimately, as discussed below, demographic factors, especially population expansion, would increase the number of individuals in and relations between these distant but not-too-remote social groups, potentially leading to the intentional use of artifacts for information exchange and the appearance of a cultural revolution.

“You say you want a revolution . . .”

Whether there was a human revolution may finally depend on what is meant by revolution. “Revolution” brings to mind the speed of political change, as in the “Russian

Revolution,” the quickness of a fashion revolution, or the abruptness of one human population replacing another. For some, a revolution happens in a day, a year, one or several lifespans (McBrearty, 2007: 134). For others it could involve tens of thousands of years (Zilhão, 2003). But the human revolution, as commonly construed, was supposed to be about abruptness, as one biological species replaced another, with dramatic differences in behavioral capacity that become manifestly expressed. We now can be sure there was no new biological species of modern humans whose appearance could explain the Middle to Upper Paleolithic changes in Europe. As discussed earlier, evidence of interbreeding implies there was no significant mean difference between the *behavioral potentials* of Neandertals and those of other penecontemporary human populations; such advantageous potentials would spread under selection. Moreover, while it cannot be denied that large and important archaeological changes occurred in Upper Pleistocene Europe (and elsewhere), the “revolutionary” aspects of them (like the artistic explosion) might best be tied to the significant changes within the Upper Paleolithic rather than at the Middle/Upper Paleolithic transition (Zilhão, 2011). But, whether or not we characterize these changes as revolutionary, they are likely reflections of something BIG. We do not believe that the ability to create the artifacts associated with “behavioral modernity” is what it means to be behaviorally modern; rather, it is the social factors that underlie their expression that are important. We believe that the changes within the Upper Paleolithic are reflections of the demographic processes that really define modernity and forever changed late Upper Pleistocene human populations. At its beginning, late Pleistocene humans were hunter-gatherers and life was initially “nasty, brutish, and short”; the end products of these changes were human populations on the verge of domesticating their foods and themselves.

Modernity as a Demographic Process

The emergence of “behavioral modernity” was triggered by demographic and social processes.

(Zilhão, 2007: 1)

Many authors have considered demography as the cause of how and why modernity emerged (e.g., Caspari, 2011; Caspari and Lee, 2004, 2006; Powell et al., 2009; Richerson et al., 2009; Shennan, 2001; Zilhão, 2007). While some suggest the possibility that the demographic change is related to climate (d’Errico and Stringer, 2011: 1067), mostly the idea is that with population growth, resources become scarcer (Stiner et al., 1999) and modern behaviors and technologies are the human response. Modern behaviors appear more often, are more persistent (for reasons discussed below), and disperse more effectively because of population growth and an increased number of interpopulational contacts (Shennan, 2001), and the rate of cultural change accelerates.

Behavioral evolution is exceptionally complex because “both genetic and non-genetic inheritance, and the interactions between them, have important effects on evolutionary outcomes” (Danchin et al., 2011: 475). We believe the relation of human demography and the emergence of modern behaviors reflects this complexity; increased adult survivorship in the Late Pleistocene influenced demographic expansions that had far reaching consequences (Caspari and Lee, 2004). This increase does not seem to have a phylogenetic basis (Caspari and Lee, 2006), but it took place in the context of other evolutionary changes and had significant population size consequences that continue to affect genetic evolution.

Recent research revealing these relationships employed a new strategy to address questions of longevity in the human fossil record, avoiding some of the problems that confront

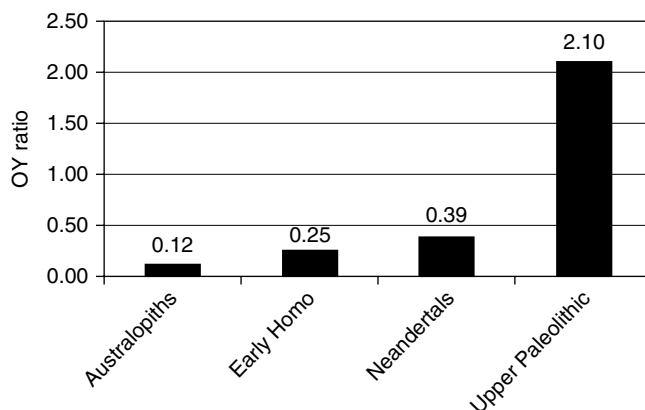


Figure 11.7. Ratios of numbers of older to numbers of younger adults (OY), results from Caspari and Lee (2004), figure adapted from Caspari and Lee (2005, Figure 1). There are significant ($p \leq 0.05$) increases between all groups, likely reflecting a Pleistocene-long trend of increased survivorship of older adults through human evolution. The increase is by far the greatest in the early modern humans of the Upper Paleolithic, when for the first time there are a larger number of older adults than younger adults in the death distribution. This is not a consequence of the increased number of burials. Although the OY ratio of early Upper Paleolithic burials is slightly higher than that of non-burials, both are significantly larger than the largest OY ratios generated from the Neandertal sample.

traditional paleodemographic analyses, problems caused by small sample size, unknown juvenile demographics, and low resolution in adult age assessment (Caspari and Lee, 2004, 2005, 2006; Trinkaus, 2011). Using the ratio of older to younger adults in the death distribution (OY ratio, Figure 11.7), a categorical approach that measures adult survivorship rather than lifespan, Caspari and Lee addressed some basic questions about the fossil record of human longevity with large aggregate samples and data resampling to assess significance. They concluded that adult survivorship was very low for much of the Plio-Pleistocene, but that OY ratios increased dramatically in the Upper Paleolithic as many adults lived to be older (Figure 11.7). This suggests the onset of major demographic change at a time of increased archaeological complexity (Caspari and Lee, 2004). Further work, comparing Middle Paleolithic Neandertals and penecontemporary modern humans from the Levant, indicated that this increase in adult survivorship was not a direct consequence of the emergence of modern humans as a taxon (Caspari and Lee, 2006) because an increase was equally associated with both of these groups. Levantine Middle Paleolithic Neandertals and modern humans had statistically identical OY ratios (approximately 1.0), significantly differing from both European Neandertals and Upper Paleolithic Europeans (Table 11.1).

The variation in OY ratios among Middle Paleolithic Neandertals reflects complexity in the relationship between material cultural traditions and longevity. Compared to European Neandertals, west Asian Neandertals have much higher adult survivorship, although both groups are associated with similar material remains. The role of differences in climate, ecology, and behavior may all be reflected in the significant difference in adult survivorship between the Neandertals of Western Asia and those of glaciated Europe, with more favorable conditions responsible for improved adult survivorship for Western Asian Middle Paleolithic groups. Favorable environmental conditions, however, cannot explain the substantially higher survivorship levels for Upper Paleolithic Europeans and makes stark the contrast between glacially adapted Neandertal and modern human demographic patterns.

Table 11.1. Average probabilities (and confidence intervals) of finding the OY ratio of one group in distributions generated from the group with which it is compared.

Comparisons		Significant Difference (Average Probability)	95% Confidence Interval (of 1,000 Probabilities Generated)
West Asian Early Moderns OY = 0.75	European Moderns (UP) OY = 2.1	YES $p \leq 0.05$	0.04–0.07
West Asian Early Moderns OY = 0.75	West Asian Neandertals OY = 1.0	NO $p \leq 0.39$	0.37–0.43
West Asian Neandertals OY = 1.00	European Neandertals OY = 0.39	YES $p \leq 0.02$ (0.016)	0.01–0.02

Differences between West Asian Middle Paleolithic groups are not significant, while West Asian groups differ significantly from both European Neandertals and modern humans of European Upper Paleolithic (UP). Adapted from Caspari and Lee (2006, Table 3).

The causes of increased longevity are likely related to its consequences through a positive feedback process. Initially the result of cultural adaptations, we posit that longevity became a prerequisite for the unique and complex behaviors that mark modernity, innovations that in turn promoted both the importance and the survivorship of older adults. Caspari and Lee (2004, 2006) suggested that adult survivorship increased in response to cultural factors promoting the importance of older adults whose experience benefited their kin groups in the harsh conditions of Upper Pleistocene Europe. The experience of older members could also underlie the material expressions associated with the Upper Paleolithic. There are a number of ways in which the demographic changes and intergenerational transfer effects associated with increased adult survivorship resulted in the complex behaviors thought to be reflected in Upper Paleolithic archaeology (Lee, 2003; Rosenberg, 2004).

In the emerging complex adaptations of the Upper Paleolithic, adult survivorship was beneficial to social groups as a whole, promoting intergenerational transfer of a variety of economic and cultural resources (Lee, 2003). In humans, as in other social species, there is transfer of resources among individuals, which contributes to the inclusive fitness of a kin group. Intergenerational transfer is particularly important for humans, where it extends over several generations. Grandparents routinely contribute economic and social resources to their descendents, increasing the fertility of their children and the survivorship of their grandchildren. The importance of the economic contributions of older adults to their social groups has been well documented (Kaplan and Robson, 2002; Hawkes, 2003). In fact, studies of living hunter-gatherers indicate that because of the skill-intensive techniques of resource acquisition, peak production rates occur in individuals over age 30 (Robson and Kaplan, 2003).

Cultural information is effectively transmitted by older members of society, reinforcing complex social connections. Multiple aspects of cultural knowledge are transmitted, from social identity to experiences dealing with unusual environmental conditions to technological innovations that promote the survival of social groups. Such knowledge is often embedded in oral traditions in which cross-generational transmission plays an important role:

Survival of periodic subsistence crises is largely dependent on a group memory of past crisis situations and of the strategies appropriate for dealing with the altered environmental conditions.

One mechanism utilized by non-literate societies for the preservation of survival knowledge is its incorporation in oral tradition. As a body of reference knowledge, oral traditions potentially operate over two time scales. Secular oral traditions (folktales, songs, and histories) depend on repetition for perpetuation with inherent potential for distortion. In contrast, sanctified oral traditions, such as ritual performances, rely on a correct reproduction of the ritual order to achieve supernatural efficacy. Rituals accordingly assume an invariant character appropriate for the transmission of survival information over extended periods of time. (Minc, 1986: 39)

Moreover, as has been recently modeled by Strimling et al. (2009), repetition—the repeated learning of cultural traits—is a critical factor in cultural learning more generally, and it has the potential to drive cultural evolution:

Here we show that repeated learning and multiple characteristics of cultural traits make cultural evolution unique, . . . We find that the possibility to predict long-term cultural evolution by some success index, analogous to biological fitness, depends on whether individuals have few or many opportunities to learn. If learning opportunities are few, we find that the existence of a success index may be logically impossible, rendering notions of “cultural fitness” meaningless. On the other hand, if individuals can learn many times, we find a success index that works, regardless of whether the transmission pattern is vertical, oblique, or horizontal. (Strimling et al., 2009: 13870)

Multigenerational families have more (and more knowledgeable) members to teach and reteach important lessons. We suggest longevity promoted the intergenerational accumulation and transfer of information that allowed for complex kinship systems and other social networks that are uniquely human.

There is a key consequence: increased adult survivorship generates population growth, the basis of the Upper Paleolithic population expansions reflected in archeological and genetic evidence (Powell et al., 2009; Shennan, 2001; Templeton, 2002). Not only does increased survivorship create the potential for greater lifetime fertility for individuals who are living longer, but the investment of older individuals in their children’s families influences their inclusive fitness both by increasing the fertility of their children and the survivorship of their grandchildren. These selective advantages promote continued population increase. The large OY ratio increase we observe is a significant factor in the evolution of modernity not only through its importance for intergenerational information transfer but because of its relationship to population expansion.

These demographic changes provide social pressures that we believe led to extensive trade networks, increased mobility, and more complex systems of cooperation and competition between groups, resulting in increased personal ornamentation, material expressions of individual and group identity, and other forms of material information exchange between groups (Wobst, 1977).

Behavioral modernity, then, is not a capacity, or an entity, but may be a response to demographic pressures, first seen on a sustained level in the European Upper Paleolithic.¹⁸ Like other aspects of modernity, we see behavioral modernity as a process. More recently, large increases in population size, associated with cultural changes that are arguably much more substantial than those seen in the Upper Paleolithic, have occurred from the Neolithic to modern times. None of these reflect a biological intellectual “capacity,” but all have a large impact on the human evolutionary process. Population growth has had major evolutionary consequences that continue to affect us biologically today and underlie the genetic meanings of modernity, discussed in the next section. The population explosion associated with domestication 10,000 years ago had its roots in the earlier demographic changes associated with what we are calling behavioral modernity, and a pattern where large numbers of people began to survive long enough to become grandparents. We therefore see increased longevity

and associated demographic changes as the fundamental link between anatomical, behavioral, and genetic modernity, an example of the impact of culture on human biology and its role in recent human evolution.

Genetic Modernity

As has been proved to be the case in the study of hominid origins, paleoanthropologists who ignore the increasing wealth of genetic data on human population relationships do so at their own peril.

(Stringer and Andrews, 1988: 1268)

Genetic, anatomical, and behavioral modernity address three different aspects of humanity related through demographic changes. Genetic modernity, like modernity in anatomy and behavior, means genetic variation similar to that found today. It is a new concept in the modern human origins discussion, made possible by the wealth of genetic information increasingly available. Like behavioral and anatomical modernity, genetic modernity has a complex origin; it does not originate at a single time or in a single place to disperse as modernity spreads (Sjödín et al., 2012). Instead, genetic modernity is expressed differently from place to place. And, like other concepts of modernity, it is difficult to define, but we begin with the precept that all living peoples are genetically modern. Genetic modernity characterizes the pattern of genetic diversity of the living human species, and understanding the origin of this pattern is central to understanding the origin of modern humans.

Can we describe any Upper Pleistocene populations as genetically modern? We think not, because like anatomical and behavioral modernity, genetic modernity comes from a process of change, in this case beginning in the Upper Paleolithic and rapidly accelerating through the Neolithic into modern times, so that the pattern of genetic diversity in living and recent humans is very different from even that of Upper Paleolithic “modern” humans. As Hawks (Hawks et al., 2007) has maintained, in terms of genetic change, agriculture was far more important than the genetic changes thought to come from “modern human origins.”

Human populations have inherited many African genes, yet we claim that modernity did not disperse around the world with genes of African descent, and that many of the features people hold in common are not directly from our common African descent. This is because the genetic changes that came after Late Pleistocene African dispersals and gene flow from Africa are at least, if not more, consequential in producing the common aspects of modern humans. These recent changes may be as great as changes in the genus *Homo* over the previous million years.

The pattern of significant changes creating genetic modernity is recent and ongoing. This pattern is one of variable, but generally little, population structure, along with increases in global population size, positive selection, and accelerating evolutionary rates. Genetic modernity has turned out to be something quite different than first envisioned when it was assumed modern humans were a new species (Stoneking and Cann, 1989).

The greatly accelerated increases in the size of the human population that created genetic modernity began before the Neolithic, but the rate massively increased during the time that humans learned to control their food resources, an acceleration continuing to the present. Two effects of the increasing population sizes changed the pattern of human genetic diversity in significant ways, such that genetic diversity today, genetic modernity as we discuss it here, is quite different from genetic diversity in the past. First, by the time of the Neolithic, expanding human population sizes and changing adaptations increased the number and scope of population dispersals. These, with their concomitant partial or complete replacements, finally came to involve virtually all human populations, whether or not they underwent economic changes associated with the Neolithic.

Neolithic Europe is a microcosm of the recent past and of the relation between past and present genetic diversity, a relationship that is important even if very significant amounts of current diversity are of recent origin. Neolithic farming reached Central Europe from the Levant by about 7,500 years ago. Genetic analysis suggests that European Neolithic populations were largely a consequence of population replacement and subsequent expansion (Fu et al., 2012): some 70% of the Neolithic settlements are of Levantine origin (Chihki et al., 2002), Neolithic hunter-gatherers of northern Europe have a genetic profile that is not often found in living populations of the region, continued gene flow between farmers from Mediterranean Europe and local and hunter-gatherer populations seems to have created current patterns of genetic variation there (Skoglund et al., 2012), and 82% of the mtDNA variants found in the earlier Central European hunter-gatherers are not found in Central Europe today (Bramanti et al., 2009). These replacements involved significant admixture with existing Europeans; “the clinal distributions of nuclear DNA and protein markers suggest that a directional expansion from the Levant is the main process reflected in the current genetic diversity” (Barbujani and Bertorelle, 2001: 23).

Similar recent expansions and local replacements with mixture occurred in many places (Gignoux et al., 2011). The large population expansions of the Holocene were not simple in situ increases of all populations. In many, perhaps most, cases, few populations expanded at the expense of many others.

The second effect of population growth has had even more influence on present genetic diversity. More people mean more mutations (Tennessen et al., 2012) and while many of these are potentially harmful, there is more opportunity for evolutionary change under selection, because some mutations are favorable. The rate of evolutionary change has accelerated in many adaptive genes (Bersaglieri et al., 2004; Dorus et al., 2004; Sabeti et al., 2006; Voight et al., 2006; Hawks et al., 2007; Williamson et al., 2007; Gilad et al., 2008; Cochran and Harpending, 2009; Moreno-Estrada et al., 2009; Prabhakar et al., 2006; Pickrell et al., 2009; Grossman et al., 2010). Acceleration has affected a wide range of genetic changes, from those influenced by disease-related selection such as sickle cell mutation in the Hemoglobin-B gene, to adaptive genes such as those governing skin pigmentation and lactase production, to genes related to changes in the human brain. We do not intend to inventory all genes known for their recent accelerated evolution; it is a rapidly growing list, and we expect that such a list would not be helpful in understanding genetic modernity. For us *it is the acceleration itself that is the most important aspect of these genetic changes that reflect genetic modernity.*

To the extent that new adaptive alleles continued to reflect demographic growth, the Neolithic and later periods would have experienced a rate of adaptive evolution > 100 times higher than characterized most of human evolution. (Hawks et al., 2007: 20756–20757)

By the beginnings of recorded history some 5000 years ago, new adaptive mutations were coming into existence at a tremendous rate, roughly 100 times more rapidly than in the Pleistocene. (Cochran and Harpending, 2009: 74)

Accelerating recent human evolution was (and for the most part still is) unexpected, and this is interesting from a history of science perspective. The relationship between the number of mutations and population size has been known for a very long time. Independently, archaeologists established the significant recent increase in human population size some time ago (cf. Hassan, 1981). Even the basic pattern of population increase—an exponential curve virtually flat for most of human prehistory and virtually vertical today—was well understood. But until just a few years ago, any link between a recent very large population size increase and an accelerated rate of evolutionary change because of many new favorable mutations was below the radar screen. It took the discovery of the actual mutations themselves to establish this relationship (Hawks et al., 2007).

It was not obvious because evolutionary stasis in modern *Homo sapiens* beginning in the Upper Paleolithic has been assumed and is still conventional wisdom. Two factors underlie this. First, stasis was almost universally expected because of the widely believed theory that modern humans appeared recently as a new species that replaced archaic species everywhere since they were better adapted. Second, the expectation of stasis followed from the widely accepted belief that the technological innovations of the Upper Paleolithic and beyond, and the consequences of complex social organization that followed the Neolithic, caused a relaxation of selection (Brace, 1995, and many others). Even though the association of domestication and the evolution of infectious diseases was well established (Cohen and Armelagos, 1984), the inherent contradiction in these two “facts”—disease evolution and the muffling of evolutionary change by selection relaxation—lay unrecognized in paleoanthropological studies. To some extent this may have been promoted by an unintended consequence of the mission of the Paleoanthropology Society to limit studies to evolutionary changes earlier than the Neolithic.

This cannot be the whole explanation, however, and the fact is that at least one paleoanthropologist understood how recent human evolution must be characterized. In the early 1970s, David Frayer was looking for references to the pattern of evolution within early modern humans of the European early Upper Paleolithic (this became the topic of his PhD dissertation in 1976) and was surprised to find that it was widely believed evolution had stopped when modern humans appeared. This was widely accepted at the time, and not just in anthropology. No less an authority than Ernst Mayr had written:

Something must have happened to weaken the selective drastically. We cannot escape the conclusion that man's evolution towards manness suddenly came to a halt. (1963; cited in Cochran and Harpending, 2009: 1)

Frayer researched this issue and subsequently wrote his dissertation (1976) that, among other things, discovered and detailed patterns and high rates of dental change in Upper Paleolithic and Mesolithic populations of Europe. Later, he showed that the rates of dental change within the European Upper Paleolithic were *even greater* than the earlier rates of change between the Middle Paleolithic (European Neandertals) and Upper Paleolithic European (“modern”) populations (Frayer, 1992). Frayer, virtually alone, had found that the rate of human evolutionary change didn't slow but had accelerated at the end of the Upper Pleistocene. It turns out that even he really underestimated how much so.

The implications of accelerated evolution can be overstated (cf. Cochran and Harpending, 2009), but it is quite clear that a good deal of the human adaptive variation now under study across the world is its consequence. How can adaptive variation result from the rapid evolution of adaptive genes? Most of this recent adaptive evolution is not in the form of classic species-wide selective sweeps (Hernandez et al., 2011) but rather was more limited and regional in scope (e.g., Bigham et al., 2010, and others) because the recent rate of expansion of the human population exceeds the ability of selection to disperse an adaptive allele, and different alleles for the same or similar adaptations have appeared in many places (Tennessen and Akey, 2011).

Genetic modernity is created by the evolutionary pattern of the last 10,000 years, brought on by the continued accelerating population size expansions and the much larger numbers of population interactions, with adaptive genes dispersing to even the most farflung populations. It was further accelerated in most places by control of food resources. Many of the genetic changes that are unique to humans happened during this period, and in the regions of highest density, population size expansions increasingly outpaced the dispersal of adaptive genes under selection so that the novel adaptations are both local (Coop et al., 2009) and convergent.¹⁹ The great majority of these changes are not old enough to have reached fixation (Hawks et al., 2007; Coop et al., 2009; Ralph and Coop, 2010).

Conclusions

The twenty-first century brought certainty to the understanding that modern humans are people alive today and their immediate ancestors. They may be described in terms of their anatomical, behavioral, and genetic modernity. Modern humans are not uniquely the descendants of a new African species that recently dispersed to replace earlier populations that lived outside of Africa. Modernity does not have this kind of phylogenetic basis; if it did, we could expect the anatomy, behavior, and genetics of modernity to appear at the same time. Instead, anatomical, behavioral, and genetic modernity have different meanings that can be understood by viewing them as different processes. Yet paleogenetics and a better understanding of the origin of modern genetic diversity demonstrate that the concepts of genetic, anatomical, and behavioral modernity are intricately related; they address three different aspects of humanity related through demography and united in the precept that all recent and living humans are modern.

This recognition creates a complex understanding of modernity because its many aspects arose as different but related gradual processes. Instead of being a discrete entity with a fixed time of origin, we see modernity as an ongoing process of change, an evolutionary *pattern* of changes that differs from archaic patterns in both tempo and mode. The modern pattern is one of increasingly rapid biological, genetic, and social changes within the widespread, interconnected human species, resulting in what might be considered three of the most unique aspects of the human species: its rapid, accelerating genetic evolution; the mixed ancestry of human populations and the absence of human races, despite widespread geographic variation (because of the existence of widespread, exogamous, genetic ties between groups); and the consequences of multigenerational relationships, grandparents, and the wider kinship/social systems they support. Here, we argue that because of this pattern, modernity can be best understood in terms of processes of biological, genetic, and social changes driven largely by demographic factors. In this chapter, we describe the processes that comprise anatomical, behavioral, and genetic modernity, three aspects of modernity interrelated through the demographic consequences of significant longevity.

Anatomical modernity has always been difficult to define precisely because modernity is a process, rather than an entity of recent African origin. We reviewed work showing that non-African fossils considered anatomically modern are neither particularly African nor particularly modern, in the sense of people living today. Instead, early anatomical modernity varies by region, a result of global trends coupled with regional variations. Africa plays a very important role in this process as the center of the human range with the highest Pleistocene population densities, but the process of modernity involved the mixture of African populations and genes with those from other regions. Because of strong directional selection at the peripheries, regional variants were also a major component of early anatomical modernity, although only some of these features persist today because of the significant demographic changes of the last 10,000 years. Anatomical variation today continues to be heavily influenced by these recent changes; many different population expansions and partial replacements are responsible for the character of modern human anatomical diversity.

Behavioral modernity is difficult to define for many of the same reasons: it also reflects an ongoing process rather than a discrete “modern” entity that appeared when the process began. For historical reasons, behavioral modernity has been equated with the European Upper Paleolithic, but the last decade has seen numerous archaeological contributions undermining the idea of a unique European “human revolution.” Instead, aspects of modernity—archaeological material interpreted as evidence of human cognitive capacity—appear in several Middle Stone Age contexts in Africa, and also at some Neandertal sites.

We argue that the European Upper Paleolithic was nevertheless very important, differing from these more ephemeral occurrences in evidence for its persistence and increasing sophistication over time.

We believe that expanding population sizes and increasing numbers, driven by great improvements in adult survivorship, underlie the archaeological manifestations of behavioral modernity. Here, we review the evidence for increased longevity in the Upper Paleolithic and discuss the economic advantages conferred by older people and the ways that longevity is linked to population growth and expansion, a social foundation for the behaviors indicative of modernity. Like anatomical modernity, behavioral modernity can be seen as an ongoing process. Our position is that the marked increase in the number of older adults reflects a shift to a modern life history pattern, one in which three-generation relationships are important, and one that results in the large-scale population expansions that underlie the pattern of genetic modernity.

The pattern of genetic variation in the human species today also has its beginnings in these Upper Paleolithic demographic changes, and the intervening history of the human species, the consequences of agriculture and domestication in most places, and exponential population growth make genetic modernity largely a product of accelerating changes in the last 10,000 years. Far from the post-Paleolithic evolutionary stasis once assumed by many, human evolution has accelerated in recent history because more people mean more mutations and more change under natural selection, a consequence of the process of modernity. Other changes are associated with the dispersal of Neolithic adaptations, population size expansions, and gene flow that include an accelerated process of local population extinctions and recolonizations. Many recently evolved genes shared by modern populations come from these changes. Again, we argue that it is not the genes themselves that make us modern but rather the accelerated process of genetic change, linked to demography. Its consequences lie in the mixed ancestry of human populations and the absence of human races.

The recognition that modernity is not a product of phylogeny permits a more nuanced view of what it means to be a modern human. Viewed from a multiregional perspective, modernity is not an entity but a consequence of biological, social, and genetic changes, linked by accelerating demographic transformations that have come to characterize living and recent humans. Emerging from a changing life history pattern characterized by increased adult survivorship, modernity is an ongoing process, a pattern of human evolution that reflects historic variation and gene flow and the dispersals of newly adaptive genes under selection. In a truly multiregional manner these continue to appear at different places and in different times, and modernity has no single origin.

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Notes

1. Humans are not the only species with a multiregional background (Ovodov et al., 2011).
2. Regionally predominant features are those very frequent in a region of the world whose persistence over time, although not necessarily to the present, independent from environmentally related selection demonstrate regional continuity.

3. Constructs such as the “Afro-European sapiens hypothesis” (Bräuer, 1984) might also be considered as a multiregional model, but the fit is not clear.
4. Other dispersals and population movements can also be distinguished, between non-African regions and in some cases from a non-African region to Africa.
5. Figures may be used to *illustrate* regional continuity; its *demonstration* comes from the comparisons of multiple observations in samples (as can be found in the references in Figure 11.1, and elsewhere).
6. From as few as one million humans in the Pleistocene (Hawks et al., 2007; Cochran and Harpending, 2009).
7. We feel confident applying the biological species concept to the interpretation of past population samples when paleogenetics demonstrates a significant pattern of mixture. The exchange of genes between populations is the fundamental basis of biological species (Mayr, 1963).
8. But not universally recognized. As our friend, the late Jan Jelinek, would often remind us: science is a *human* activity.
9. In the d’Errico and Stringer citation, the authors specifically address a *phylogenetic* issue, the issue of ancestry, in their assertion that all living humans are not uniquely the descendents of a small African population. In context, they clearly also include Neandertals in the ancestry of at least some populations. No matter how one or both of the authors may choose to define species, and address whether or not species so-defined can significantly (their word) interbreed, we are not addressing species but the issue of multiple ancestry, and the phylogenetic interpretation of this position is evident.
10. Citing Hawks and Cochran (2006: 102): “Genetic introgression, or ‘introgressive hybridization,’ is classically taken as the introduction of alleles from one species into another species through hybridization (Anderson and Hubricht 1938). However, because species and subspecies boundaries are often imprecisely known, or fuzzy in nature, naturalists often adopt a more permissive definition [of introgression] that encompasses gene flow between subspecies, races, or varieties in addition to species (Rieseberg and Wendel, 1993).”
11. These percentages reveal a far greater genetic heritage than the “genetic swamping” suggested by Relethford (2003) when only mtDNA data were known.
12. “Crossing is not a late human acquisition which took place only when man had reached his modern phase, but must have been practiced ever since man began to evolve” (Weidenreich, 1946: 82).
13. We would expect that if the origin of the moderns in either or both of these regions was the result of a complete replacement by peoples of African descent, most or all of the modern differences would be found with the local archaic samples.
14. Merging parts of two of João Zilhão’s paper titles (2006b, 2010a).
15. This is an assumption of the Assimilation Model.
16. Mellars (2006), for instance, recently reiterated the widely held position that the Upper Paleolithic represents so many complex innovations (including an emphasis on blades and new types of complex tools made of bone, antler, and ivory indicating vastly improved technology, many objects of personal adornment, complex and varied art forms including engraving, sculptures, cave paintings, and musical instruments, exotic raw materials, and other evidence of long-distance distribution and trade) that it can only be explained by significant cognitive differences between modern humans and Neandertals.
17. Speth (2005), for instance, suggests that differences between Middle and Upper Paleolithic assemblages do not speak to cognitive differences; using examples from North American Paleo-Indian and Early Archaic periods, he shows that if interpreted the same way as Paleolithic sites, differences in the archaeological remains of some recent, obviously modern humans would also indicate differences in cognitive potential!
18. And we believe no doubt in many other places where the large samples and dense archaeological remains required to demonstrate these changes have not yet been found.
19. “Convergence” is used here in the same sense as in phylogenetics, meaning the same adaptation appears independently in different geographic regions because of different mutations, as in the sense of Bigham et al. (2010).

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Chapter 12

The Paleobiology of Modern Human Emergence

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Introduction

Through the discussions of modern human emergence of the past century, there has been an undercurrent that there is something adaptively, evolutionarily, behaviorally superior about modern humans. After all, by ~35,000 years ago (all ages are in calendar years), all known humans were anatomically “modern,” with the possible exception of the human remains from Liang Bua in insular Southeast Asia. In evolutionary time, the final transition from late archaic to modern humans took place relatively rapidly, in ≤ 10 ka in many regions where the dating is sufficiently precise and in < 50 ka in all regions for which sufficient fossils exist.

Since the general recognition in the late nineteenth century of a sequence of Paleolithic technocomplexes in western Eurasia and that the Neandertals both preceded modern humans in time and were an extinct group of humanity, the inherent superiority of modern human biology has been taken for granted. This has been implicit, sometimes explicit, independent of whether the phylogenetic interpretations were in terms of population continuity between late archaic and early modern humans or involved the emergence of modern human biology in one region and its subsequent replacement of late archaic human biology elsewhere. At times, archeological manifestations of this evolutionary advantage were cited, mostly reflecting the cultural and technological elaborations of the Upper Paleolithic (*sensu lato*), and occasional inferences from human biology were made to account for the superiority of modern humans (or as often the inferiority of late archaic humans).

These issues were reformulated a quarter of a century ago into an explicit question as to why modern human anatomy became the dominant form of human biology within a relatively short evolutionary time in the Late Pleistocene. This coincided with a refocus on Late Pleistocene human paleontology and combined with an emphasis in Paleolithic archeology on the behavioral implications of the archeological record. Since then, perspectives on the paleobiology of modern human emergence have evolved. The same issues remain, but many of the inferences that appeared straightforward are now less readily apparent. It is therefore appropriate to reassess the changes in human behavior, as reflected principally in

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aspects of human biology, that occurred with the emergence and establishment of the morphological gestalt of living humanity.

The question is therefore the nature of the behavioral similarities and differences between late archaic and early modern humans, from the earliest emergence of the latter in the late Middle Pleistocene to their eventual domination by ~35 ka BP. Even though most adaptive behaviors were interrelated, they are assessed here with respect to population dynamics, locomotion, energetics, manipulation, stress and survival, “behavioral modernity,” and life history issues. These considerations follow a review of the changes of the past quarter century in the framework for such assessments.

The Later Twentieth Century Perspective

The 1970s–1980s

The 1970s saw a resurgence of interest in modern human emergence and the Neandertals, with the first serious reevaluations of original fossils (other than descriptions of new remains) since the 1920s. This interest led to conference volumes (e.g., Trinkaus, 1983a, 1989a; Mellars and Stringer, 1989) (with more through the 1990s) and review articles (e.g., Brose and Wolpoff, 1971; Howells, 1975; Trinkaus and Howells, 1979; Smith, 1982; Hublin, 1983; Trinkaus, 1986; Stringer and Andrews, 1988), highlighted by the 1984 volume on *The Origins of Modern Humans* (Smith and Spencer, 1984). The last in particular laid out most of the key paleontological issues for the subsequent decades. It is relevant to summarize the perspectives of that time.

The now-dominant out-of-Africa phylogenetic models were in their naissance, having been proposed based on the “tropical” limb proportions of European early modern humans (Trinkaus, 1981) and the early appearance of modern humans in sub-Saharan Africa (Bräuer, 1982). Adequate dating and/or diagnostic morphology of early modern humans in Africa was then rare, but it was supported by early ages available for the Omo-Kibish fossils (Butzer et al., 1969) and the morphology of Omo-Kibish 1 (Day and Stringer, 1982). Extant human molecular data only played a role at the end of the 1980s (Cann et al., 1987; Stringer and Andrews, 1988).

Even though suggestions existed for an early, Marine Isotope Stage (MIS) 5 age for the Qafzeh early modern humans (Bar-Yosef and Vandermeersch, 1981; but see Jelinek, 1981, 1982), it was not until later that secure early dates for Qafzeh (Valladas et al., 1988) and then Skhūl (Stringer et al., 1989) became available. It was therefore reasonable (e.g., Trinkaus, 1986) to assume an archaic-to-modern chronological sequence within each geographical region of the Old World.

Although it was recognized that early modern humans in Southwest Asia were associated with Middle Paleolithic technocomplexes (Howell, 1958; Vandermeersch, 1981; Trinkaus, 1984a) and that late Neandertals in Europe made Initial Upper Paleolithic assemblages (Lévêque and Vandermeersch, 1980; see also Leroi-Gourhan, 1958), it appeared reasonable to view these culture-biology “anomalies” as part of the complexities of the “transition” that could be glossed over in looking at the larger issues of modern human behavioral emergence.

There was a general acceptance of a series of European fully “modern” human fossils (other than teeth) as being associated, or contemporaneous, with the Aurignacian (Cioclovina, Cro-Magnon, La Crouzade, Hahnöfersand, Mladeč, La Rochette, Les Rois, Velika Pečina, Vogelherd, Zlatý kůn, and possibly Muierii). Of these remains, the Cioclovina, La Crouzade, Mladeč, Muierii, and Les Rois fossils have retained their (albeit late)

“Aurignacian” contemporaneity (Wild et al., 2005; Soficaru et al., 2006, 2007; Henry-Gambier and Sacchi, 2008; Ramirez Rozzi et al., 2009), the Cro-Magnon and La Rochette samples are Mid Upper Paleolithic (Gravettian) (Henry-Gambier, 2002; Orschiedt, 2002), the rest are either terminal Pleistocene or Holocene in age (Smith et al., 1999; Terberger et al., 2001; Svoboda et al., 2002; Conard et al., 2004), and none dates to the earliest phases of the Aurignacian.

The more paleobiological issues were concerned mostly with issues of “robusticity.” The Neandertals were seen as markedly robust (e.g., Smith, 1983; Trinkaus, 1983b,c). The apparently more gracile early modern humans, both the Middle Paleolithic ones from Qafzeh and Skhul and earlier Upper Paleolithic European ones, were inferred to reveal a significant decrease in strength, endurance, and general use of human anatomy to accomplish tasks (cf. Smith, 1983; Trinkaus, 1986). This shift was evident from the teeth to the toes.

Changing Perspectives 1990s–2000s

Chronology

First and foremost, the chronology of modern human appearance has evolved substantially and continues to do so. In the late 1980s, the earlier Late Pleistocene (MIS 5) age of the Qafzeh and Skhul samples was confirmed (Valladas et al., 1988; Stringer et al., 1989). These dates were followed by a slightly older MIS 5 age for Tabun 1 and an earlier (MIS 6) age for the layer C Tabun 2–7 archaic humans (Mercier et al., 1995; Grün and Stringer, 2000). These changes indicated a process of alternating human occupation of Southwestern Asia through MIS 6–3 (cf. Stefan and Trinkaus, 1998), paralleling the Afro-Arabian versus Palearctic faunal shifts evident in extreme Southwest Asia (Tchernov, 1998). In addition, it has been documented that early modern humans were present in MIS 6 at Omo-Kibish and Herto in equatorial East Africa (White et al., 2003; McDougall et al., 2005), despite a mix of more archaic (Herto 1 and Omo-Kibish 2) and distinctly modern (Herto 5 and Omo-Kibish 1) remains (Day, 1969; White et al., 2003).

These early modern human ages have been joined by ongoing discussions of the MIS 5–4 Middle Stone Age (MSA) remains from Southern Africa, which exhibit a complex mix of predominant archaic and occasional modern human features; their ages are not in question—only whether they qualify as “modern” humans (Rightmire and Deacon, 1991; Smith, 1993; Lam et al., 1996; Churchill et al., 1996; Grine et al., 1998; Schwartz and Tattersall, 2002; Liu et al., 2010a). Similarly, the Middle Paleolithic ages of the Aterian remains from Northwest Africa have been substantiated (Débénath, 1994), but (despite a tendency to include them within “modern humans” [e.g., Bräuer, 2008]), they present an abundance of archaic plus occasional purportedly modern human features (Vallois and Roche, 1958; Ferembach, 1976, 1998; Hublin and Tillier, 1981; Harvati and Hublin, 2009). In both of these samples, the emphasis has been on whether they are Neandertals rather than whether they exhibit distinctive, derived, modern human morphology (cf. Trinkaus, 2006b). They are best considered as late archaic humans with occasional features that make them appear more “modern” or (more appropriately) “non-Neandertal.”

In Europe, as noted, most of the “earliest” Upper Paleolithic modern humans have been directly dated to later in the Pleistocene or to the Holocene, leaving a later Aurignacian sample consisting of the Cioclovina, La Crouzade, Mladeč, Muierii, La Quina Aval, and Les Rois remains, plus isolated teeth (Teschler-Nicola, 2006; Soficaru et al., 2007; Henry-Gambier and Sacchi, 2008; Ramirez Rozzi et al., 2009; Doboş et al., 2010; Verna et al., 2012). The earlier phases are represented only by the Oase fossils plus more recent teeth and phalanges from Brassempouy (Henry-Gambier et al., 2004; Trinkaus et al., 2013);

the fragmentary Kent's Cavern 4 maxilla may belong with this group (Higham et al., 2011; but see White and Pettitt, 2012). At the same time, the dating and analysis of the stratigraphically higher portion of the Palomas sample (Walker et al., 2008) has shown that Neandertals, as well as Middle Paleolithic technology (Straus, 2005; Zilhão, 2006), persisted millennia later in Iberia south of the Pyrenees than elsewhere in Europe (confirming earlier suggestions from Zafarraya [Hublin et al., 1995] despite dating uncertainties [Barroso-Ruiz, 2003]). Moreover, the association of Neandertals with Initial Upper Paleolithic technocomplexes has been supported for Western Europe (Miskovsky and Lévêque, 1993; Hublin et al., 1996; Bailey and Hublin, 2004; Semal et al., 2009; Crevecoeur et al., 2010; Soressi, 2010) and further east within Europe (Harvati et al., 2003), despite comments to the contrary (Bar-Yosef and Bordes, 2010).

In eastern Eurasia, the ages of the latest archaic humans has remained elusive, although specimens date into MIS 3 in Central Asia and southern Siberia (Shpakova, 2005; Glantz et al., 2008) and into MIS 5 in portions of China (Wu et al., 2013). However, the Tianyudong and Niah Cave remains have established modern human presence in East Asia by 40 ka BP (Barker et al., 2007; Shang and Trinkaus, 2010), and the Tam Pa Ling cranium pushes it back 50–60 ka BP in Southeast Asia (Demeter et al., 2012). Moreover, the Zhiren 3 mandible takes one distinctive aspect of modern human anatomy (a “chin”) back to ~110 ka BP in south China (Jin et al., 2009; Liu et al., 2010a).

Population Processes

The past few decades have been dominated by arguments concerning who had sex with whom in the Late Pleistocene. Although out-of-Africa with assimilation was proposed initially (Trinkaus, 1981; Bräuer, 1982; Smith et al., 1989), it was eclipsed by a debate between out-of-Africa with total replacement of regional archaic human populations versus Regional Continuity with interregional gene flow (“Multiregional Evolution”). Two-and-a-half decades of debate ensued, involving fossils, recent and ancient human DNA, shifting chronologies, and competing analytical algorithms. The field has come to the general consensus that modern human biology emerged in the late Middle Pleistocene of equatorial Africa and subsequently spread through population dispersal and/or gene flow. The process is best characterized by an Assimilation Model (Smith et al., 1989, 2005; cf. Trinkaus and Zilhão, 2002; Trinkaus, 2005b, 2007; Smith, 2010). Questions remain as to how much assimilation/gene flow took place, where, and when. The uncertainties are in part due to the dearth of diagnostic fossil remains, especially in critical time periods and regions. They are also influenced by ongoing debates concerning aspects of morphology and, increasingly, aDNA.

Functional Anatomical Shifts

The functional interpretations of morphological changes between late archaic (still mostly Neandertal) and early modern humans have shifted and been refined. There has been concern with the scaling of bone strength, thereby generating more appropriate measures of “robusticity” (or strength above baseline levels) (Ruff et al., 1993). Assessments of muscle moment arm effectiveness (or effective mechanical advantages—EMAs) have partially moved beyond looking only at the power arm (Trinkaus and Villemeur, 1991; Villemeur, 1994; Anton, 1994; Trinkaus and Rhoads, 1999; O'Connor et al., 2005; Churchill and Rhodes, 2006; Maki and Trinkaus, 2011). Variation in body shape, as an independent variable, has been increasingly incorporated (Ruff et al., 1993; Ruff, 1995; Trinkaus and Rhoads, 1999; Trinkaus et al., 1999; Trinkaus, 2000). It has been recognized that many of the adult patterns are the products of activity levels and patterns during development (Trinkaus, 1993a; Pearson and Lieberman, 2004; Cowgill, 2010). There have been efforts to assess

whether the morphological variation is a genetic marker or a reflection of behavioral patterns (e.g., axillary border variation [Trinkaus, 2008a; Willman and Franciscus, 2010]). There have been attempts to correlate changes in morphology, especially within the upper limb, with changes in technology (Niewoehner, 2001; Churchill and Rhodes, 2009; Trinkaus, 2008b). The analyses have incorporated internal skeletal morphology, including cross-sectional geometry and trabecular orientations (e.g., Trinkaus et al., 1991; Trinkaus, 2000; Cowgill, 2010; Scherf and Hublin, 2010), and higher resolution techniques are being applied (e.g., Puymeraul, 2011).

These shifts provide a more complex perception of changes in the habitual behavior as reflected in human skeletal biology. Issues remain as to the appropriate scaling of various parameters, within the limits of fossil preservation, but functional interpretations have moved beyond assessments of modern human emergence as a “robusticity transition.”

Early Modern Human Paleobiology

Despite efforts to integrate Upper Paleolithic fossils into phylogenetic debates (Freyer, 1978; Wolpoff, 1980; Smith, 1982), paleobiological considerations of early modern humans have lagged behind those of late archaic humans. Comparative analyses of individual complexes (e.g., Churchill, 1994; Hambücker, 1993; Holliday, 1997a; Franciscus, 1995, 2003; Holt, 2003; Trinkaus and Rhoads, 1999; Trinkaus, 2000, 2005a), plus analyses of MIS 3 early modern remains (e.g., Zilhão and Trinkaus, 2002; Teschler-Nicola, 2006; Trinkaus and Svoboda, 2006; Crevecoeur, 2008; Henry-Gambier and Sacchi, 2008; Doboş et al., 2010; Shang and Trinkaus, 2010; Bayle et al., 2010), have increasingly (but not universally) viewed the Late Pleistocene transition from both sides, not just one of late archaic versus late Holocene human biology. As a result, many of the purportedly “archaic” or “Neandertal” features previously emphasized have turned out to be “Late Pleistocene” and contrast primarily with sedentary Holocene humans. Yet it is still common to compare Middle Paleolithic paleobiology solely to Holocene human variation, an approach that carries the assumption that functional anatomy and behaviorally induced variation has not changed among modern humans since MIS 3.

At the same time, redating of specimens and additional focus on Upper Paleolithic remains have highlighted the dearth of Early Upper Paleolithic human remains, combined with the overrepresentation of craniofacial and dental remains in that sample (cf. Bailey et al., 2009). There are only three associated partial skeletons from that time period (Muerii 1, Nazlet Khater 2, and Tianyuan 1 [Crevecoeur, 2008; Doboş et al., 2010; Shang and Trinkaus, 2010]); the first is very incomplete, and the other two have variably pathological lower limbs. As a result, most paleobiological analyses compare Middle Paleolithic (MIS 5–3) Neandertals to Middle Paleolithic (MIS 5b) and/or Mid Upper Paleolithic (post-35 ka BP MIS 3) modern humans, with only passing reference to those who actually succeeded late archaic humans in time.

Stress and Survival

Considerations of pathological abnormalities of Late Pleistocene humans have shifted from an inconvenience to a source of data on patterns and levels of stress and, given the “osteological paradox” (Wood et al., 1992), of survival. Monographs on samples (e.g., Trinkaus, 1983c; Bar-Yosef and Vandermeersch, 1991; Alexeeva et al., 2000; Zilhão and Trinkaus, 2002; Trinkaus and Svoboda, 2006; Crevecoeur, 2008; Shang and Trinkaus, 2010) routinely include paleopathological assessments, and differential diagnoses of abnormalities are increasingly available (e.g., Crubézy and Trinkaus, 1992; Formicola et al., 2001; Formicola and Buzhilova, 2004; Tillier et al., 2001; Smith et al., 2006; Crevecoeur and Villotte, 2006;

Trinkaus et al., 2008; Trinkaus and Pinilla, 2009; Walker et al., 2010; Trinkaus and Buzhilova, 2012). There have been assessments of differential levels and/or patterns of stress (Ogilvie et al., 1989; Brennan, 1991; Skinner, 1996; Guatelli-Steinberg et al., 2004; Berger and Trinkaus, 1995; Villotte, 2008), although the comparisons remain principally between Neandertals and Holocene humans. There are also social implications for differential survival (Lebel and Trinkaus, 2002). However, the ultimate issues in relating these paleopathological analyses to Late Pleistocene human behavior concern inferring levels of stress, possible loss of function, and the implications for survival (Wood et al., 1992; Trinkaus, 2006a), since most of the lesions imply some level of survival.

Archeological Correlations

These human paleobiological changes exist in a Paleolithic context, and they have been accompanied by discussions of the emergence of “behavioral modernity,” what is it, who had it, and in what context(s) (biological, geographical, and chronological) did it emerge (e.g., McBrearty and Brooks, 2000; d’Errico, 2003; Henshilwood and Marean, 2003; Zilhão, 2007; Norton and Jin, 2009; Klein, 2009; Zilhão et al., 2010; Teyssandier et al., 2010; Shea and Sisk, 2010; Shea, 2011). Unfortunately, there has been a persistence of an earlier paradigm (e.g., Breuil, 1912) that equates “behavioral modernity” with “anatomical modernity,” even in the face of absent or morphologically ambiguous human remains. As such, it operates in both directions, with anatomically “modern” fossils implying behavioral advancement and behaviorally “modern” archeological remains being used as evidence of modern human biology. Such a paradigm was long ago rejected in socio-cultural anthropology (cf. Boas, 1940), and it is time that paleoanthropology moved beyond it.

Implications of Paleobiological Complexes

Given these considerations, it is appropriate to review current inferences regarding the nature of changes in human behavioral patterns with the emergence of modern humans, as reflected in their paleobiology in their archeological context.

Samples of Concern

The samples of concern are those that bracket the transition from late archaic to early modern human biology. They vary considerably in completeness, chronological security, geographical distribution, and paleobiological relevance.

The initial such transition took place within the terminal Middle Pleistocene of equatorial Africa (Day and Stringer, 1982; White et al., 2003; Pearson et al., 2008a,b; Bräuer, 2008), but paleobiologically informative remains are rare from the relevant samples. They consist of the fragmentary Omo-Kibish fossils, the KNM-ER 999 femur, and (possibly) the undated Loiyangalani remains (Twisselmann, 1991; Trinkaus, 1993b; Pearson et al., 2008a,b; Muteti et al., 2010). To this sample are added the abundant MIS 5b Southwest Asian Qafzeh and Skhul remains (McCown and Keith, 1939; Vandermeersch, 1981; Tillier, 1999). They are collectively referred to here as Middle Paleolithic modern humans (MPMH). The MIS 5 South African MSA and Northwest African Aterian remains are predominantly late archaic and are included as special cases, as are the (probably) earlier East African Singa 1 and ES-11693 crania (Bräuer and Leakey, 1986; Spoor et al., 1998).

In Western Eurasia, the late archaic sample is, of course, the Neandertals, here restricted to MIS 5–3 remains. With few exceptions, relevant remains are Middle Paleolithic associated.

The principal exceptions are the Saint-Césaire, Spy, and Lakonis remains associated with the Initial Upper Paleolithic (IUP, including the Ahmarian, Bohunician, Châtelperronian, Lincombian, and Uluzzian technocomplexes, among others). Moreover, the late sub-Pyrenean Iberian Neandertals, who were contemporaneous with Early Upper Paleolithic modern humans farther north (Walker et al., 2008), are associated with the Middle Paleolithic. In Eurasia east of $\sim 50^\circ$ E longitude, late archaic humans are represented by possibly Neandertal incomplete remains from Central Asia and Siberia (Gremyatskij and Nesturkh, 1949; Shpakova, 2005; Coppens et al., 2008; Glantz et al., 2008), plus MIS 5 East Asian fragmentary craniofacial and dental remains (Wu and Poirier, 1995; Liu et al., 2010b).

Post-50 ka BP early modern humans in Eurasia (plus Northeast Africa) are represented principally by two samples, a small Early Upper Paleolithic (*sensu lato*) sample (EUP; $\sim 40\text{--}\sim 35$ ka BP; including Aurignacian-associated and contemporaneous non-Western Eurasian remains) and a much larger Mid Upper Paleolithic (*sensu lato*) sample (MUP; $\sim 35\text{--}\sim 25$ ka BP). The former sample is primarily craniofacial and dental (with the exceptions of the Muierii, Nazlet Khater, and Tianyuan associated partial skeletons and the Mladeč unassociated postcrania) and scattered geographically. The MUP sample includes remains principally from burials across Europe and into Southwest Asia, plus scattered remains from Eastern Asia. Added onto these samples are MIS 5c fossils from Zhirendong.

Populational Issues

The perpetual debate on the population processes accompanying modern human emergence, plus the chronological framework for the appearance and establishment of early modern humans across the Old World, have implications for behavioral assessments of modern human emergence.

As noted above, the field is reaching a consensus that some version of the Assimilation Model (Smith et al., 1989) best characterizes the population processes of modern human origins. The degree of admixture, and when and where it occurred, remains debated, but paleontological, ancient DNA and recent human DNA analyses no longer fail to find evidence of non-equatorial-African ancestry in Eurasian early and recent modern humans (Trinkaus, 2007; Smith, 2010; Green et al., 2010; Liu et al., 2010a). The paleobiological implication is that late archaic and early modern humans saw each other as sufficiently close behaviorally and socially to view the other as appropriate mates.

The process appears to have initially involved the gradual emergence of modern human biology from earlier archaic humans in sub-Saharan Africa in the late Middle Pleistocene (MIS 7–6). This was followed by various earlier Late Pleistocene expansions, through population dispersal and/or gene flow, across at least Southern Asia by MIS 5c (as indicated by Zhiren 3) and possibly into Southern Africa (as indicated by some more modern features in the South African MSA archaic human remains). The modern human occupation of the Eastern Mediterranean littoral was temporary, since the region was occupied by archaic humans in early MIS 5, by modern humans in mid MIS 5, and then reoccupied during MIS 4–3 by late archaic humans. However, the occupation of Southeastern Asia appears to have been more permanent, as documented by Tam Pa Ling. The occupation of most of the remainder of Eurasia by modern humans, including Southwest Asia, all of Europe, and Asia north of $\sim 35^\circ$ N latitude, appears to have occurred only after ~ 50 ka BP; the earliest well-dated modern humans in the regions (Oase in the west and Tianyuan in the east) (Trinkaus et al., 2013; Shang and Trinkaus, 2010) being $\sim 40,000$ years old. The final occupation of Eurasia occurred in Iberia, south of the Pyrenees, after ~ 40 ka BP and possibly as late as ~ 34 ka BP (Zilhão, 2006; Walker et al., 2008). Neandertals also persisted until at least ~ 37 ka BP in Northwestern Europe (Semal et al., 2009) and possibly as late as ~ 36 ka BP in

parts of Central Europe (Higham et al., 2006). There is no current direct or indirect evidence for late archaic humans after ~34 ka BP.

This chronological and geographical pattern of the appearance/establishment of modern human biology has one fundamental implication for the paleobiological transition. Whatever adaptive advantage early modern human biology may have conferred, it was extremely subtle and was frequently overridden by other pressures. Modern human biology was in equatorial Africa for $\geq 50,000$ years before it expanded outward. It appears to have spread relatively rapidly across Southern Asia, given its appearance at both ends by ~100 ka BP. However, it was not sustained in Southwestern Asia, and it coexisted with late archaic human morphology farther north in Asia for $\geq 50,000$ years. There is only evidence of archaic humans in Western Asia north of 35° N latitude or in Europe prior to ~40 ka BP. Despite its presence in Western Europe north of the Pyrenees by ~40 ka BP, it took ~5,000 years to penetrate Iberia and possibly as long to reach the North Sea. It is also unclear how long it took modern human biology to reach South and Northwest Africa, but fully modern humans are currently absent there > 50 ka BP. The spatiotemporal evidence, despite limitations, therefore contradicts any model that invokes a sweeping expansion of modern human biology.

At the same time, several lines of evidence suggest that modern human establishment involved substantial population increases. The earliest modern human fossils, despite the indications of some level of assimilation, have a total morphological gestalt that is the derived pattern of modern humans (cf. Trinkaus, 2006b). Their immediate ancestry therefore must have been predominantly that of earlier “modern” humans. Emerging stable isotopic data, especially $\delta^{15}\text{N}$ and $\delta^{34}\text{S}$ (Hu et al., 2009; Richards and Trinkaus, 2009; Trinkaus et al., 2009), imply a dietary expansion toward more labor intensive, smaller package food resources (despite equivocal archeological evidence), presumably from greater population pressure on resources (see also Villaverde et al., 1996; Stiner et al., 1999; Kuhn et al., 2009). At least in Europe, the decline of cave bear (*Ursus spelaeus*) populations through MIS 3 (Pacher and Stuart, 2009) may have been due in part to expanding human populations (Grayson and Delpech, 2003), although that process began before the transition to modern humans (Stiller et al., 2010). And the major increase in personal decoration and symbolic items through the IUP and EUP, relative to their rare and scattered occurrence in the Middle Paleolithic (see below), has been taken to reflect augmenting social pressures from population expansion (e.g., Hovers and Belfer-Cohen, 2006; Zilhão, 2007; Straus, 2010).

These inferences combine to indicate a pattern of changing population pressures during the pan-Old World establishment of modern human biology, but ones that emerged in fits and starts and took many tens of millennia to occur.

Locomotion and Landscape Use

Locomotor Robusticity

The emergence of modern humans was formerly described in terms of a significant reduction in overall strength and endurance (Trinkaus, 1976a, 1983b, 1986). However, the realization that anatomical strength must be scaled to baseline loads, in particular body mass times its effective moment arm (Ruff et al., 1993), taken in the context of contrasting body shapes between Neandertals and more linear Southwest Asian and European early modern humans (Trinkaus, 1981; Ruff, 1994; Holliday, 1997a,b), has led to a reassessment of the degree of change in locomotor strength and endurance. When appropriately scaled, despite the approximate nature of body mass estimations (Auerbach and Ruff, 2004), overall femoral and tibial diaphyseal robusticity changed little with the emergence of modern humans (Ruff et al., 1993; Trinkaus and Ruff, 1999a,b, 2012; Trinkaus, 2000, 2006c; Shang and Trinkaus,

2010). Moreover, there was little change in lower limb robustness through MIS 3–2 and into non-sedentary Holocene populations (Holt, 2003; Shackelford, 2007). The same applies to effective moment arms for quadriceps femoris at the knee (Trinkaus and Rhoads, 1999) and for triceps surae at the ankle (Trinkaus, 2006c), as well as with respect to anterior femoral curvature (Shackelford and Trinkaus, 2002).

Earlier suggestions of greater femoral antero-posterior reinforcement among early modern humans (plus the IUP Saint-Césaire Neandertal), implying higher levels of long-distance mobility (Trinkaus, 1986; Trinkaus et al., 1999), are no longer supported (Trinkaus and Ruff, 2012; Trinkaus, in press b). That inference was based on differences in midfemoral diaphyseal shape, in which Neandertals (and archaic *Homo* generally [Trinkaus, 1984b; Ruff et al., 1993; Trinkaus and Ruff, 2012]) have subcircular cross-sections that are, on average, relatively broader than deep, reflected in their antero-posterior versus medio-lateral second moments of area (Figure 12.1a). However, tibial diaphyses do not support a difference in their relative maximum (antero-posterior) to minimum (medio-lateral) second moments of area across the samples (Figure 12.1b). If the femoral midshaft antero-posterior rigidity is scaled to baseline loads (estimated body mass times femur length) (Figure 12.1c), any difference disappears. The remaining contrast is in terms of relative medio-lateral rigidity (Figure 12.1d), which may well be secondary to differences in pelvic proportions (Trinkaus, 1976b, 2011a; Rosenberg, 1988; Rak, 1991; Ponce de León et al., 2008) given the biomechanical effect of pelvic breadth on femoral diaphyseal medio-lateral reinforcement (Ruff, 1995).

The same patterns of relative diaphyseal rigidity are evident in the immature femoral and tibial diaphyses (Trinkaus et al., 2002a; Cowgill, 2010). This developmental consistency in implied levels of locomotor activity and burden carrying is reinforced by the consistently low femoral neck-shaft angles across late archaic, EUP, and MUP samples (Trinkaus, 1993a; Shang and Trinkaus, 2010), which reflect elevated levels of crural loading during development (Anderson and Trinkaus, 1998). The exception to this pattern is the immature and mature MPMH from Qafzeh and Skhul plus KMN-ER 999 (Trinkaus, 1993a,b; Tillier, 1999). The high MPMH neck-shaft angles may be due in part to their linear body shapes (Weaver, 2000); however, that relationship is insufficient to account for the degree of difference, and it is contradicted by the low neck-shaft angles yet linear bodies of the Eurasian EUP and MUP samples (Holliday, 1997a; Trinkaus, 2006c; Trinkaus et al., 2006a; Shang and Trinkaus, 2010).

Lower Limb Abnormalities

The importance of locomotor endurance through the Late Pleistocene is reflected in pathological patterns among both late archaic and early modern humans. Despite the high incidence of traumatic lesions among at least late archaic humans (Wu et al., 2011), none of the Late Pleistocene humans sustained lower limb injuries that would have kept them from being mobile on the landscape. The oldest such injuries known are the terminal Pleistocene Vado all'Arancio 1 and the initial Holocene Veyrier 1 (Pittard and Sauter, 1946; Holt et al., 2002). Healed lower limb injuries among late archaic and early modern humans are fractures of fibulae and metatarsals, plus marked osteoarthritis of weight-bearing articulations (McCown and Keith, 1939; Heim, 1982a; Trinkaus, 1983c, 1985; Berger and Trinkaus, 1995). None of these would have prevented locomotion, however painful they might have been. In addition, several individuals with pronounced developmental or degenerative lower limb abnormalities, the Shanidar 1 Neandertal (Trinkaus, 1983c), the EUP Nazlet Khater 2 and Tianyuan 1 (Crevecoeur, 2008; Shang and Trinkaus, 2010), and the MUP Dolní Věstonice 15 and Sunghir 3 (Buzhilova, 2000; Mednikova, 2000; Trinkaus et al., 2001, 2006b; Formicola and Buzhilova, 2004), maintained lower limb strength levels similar to or above those of normal Late Pleistocene individuals.

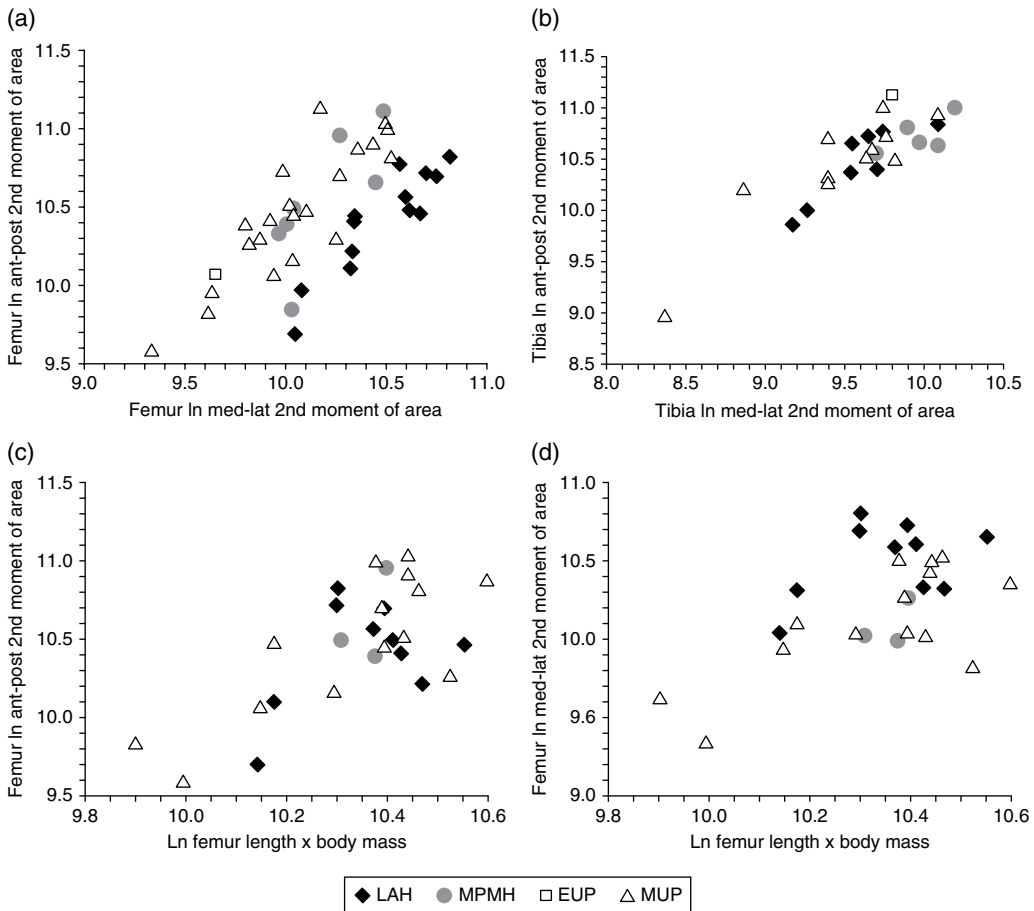


Figure 12.1. Midshaft cross-sectional parameters for Late Pleistocene human femora and tibiae. (a) Femur antero-posterior versus medio-lateral second moments of area. (b) Tibia antero-posterior versus medio-lateral second moments of area. (c) Femur antero-posterior second moments of area versus femur length times estimated body mass. (d) Femur medio-lateral second moments of area versus femur length times estimated body mass. LAH: late archaic humans; MPMH: Middle Paleolithic modern humans; EUP: Early Upper Paleolithic modern humans; MUP: Mid Upper Paleolithic modern humans. The only contrasts are in femoral antero-posterior versus medio-lateral relative second moments of area and its medio-lateral second moment of area versus length times body mass, most likely due to contrasts in body shape.

Mobility was therefore essential for all of these groups, and individuals with debilitating lower limb injuries did not enter the paleoanthropological record.

Human Energetic Issues

Concerns with Energetics

There have been attempts to characterize the energetic demands of Late Pleistocene humans, usually through the calculation of daily energy expenditure (DEE) values for individuals based on body mass estimates, plus gender and climatic parameters (e.g., Sorensen and

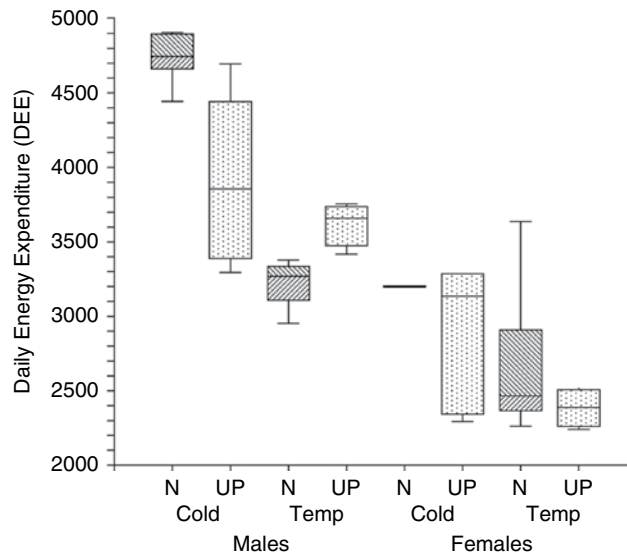


Figure 12.2. Distributions of daily energy expenditure (DEE, in kcal/day) estimates for Late Pleistocene humans, following the criteria of Froehle and Churchill (2009) and using their formulae for estimating basal metabolic rate (BMR) from body mass and its conversion to DEE based on physical activity levels (PALs) and climate zone. Only specimens with body masses derived from femoral head diameter are employed (average of values from the formulae of Ruff et al. [1991] and Grine et al. [1995]), to avoid uncertainties with body shape assessments when bi-iliac breadth is unknown. Only non-pathological specimens securely assigned to MIS 5–3 are included. Sexes, body masses, climatic parameters and samples corrected from Froehle and Churchill (2009). For the PAL values, those with estimated mean annual temperature (MAT) < 10°C are considered “cold,” and those with MAT > 10°C are considered “temperate” or “tropical.” N: MIS 5–3 Neandertals; UP: MIS 3 EUP and MUP modern humans.

Leonard, 2001; Steegmann et al., 2002; Aiello and Wheeler, 2003; Froehle and Churchill, 2009). In these assessments, it is primarily the resultant high DEE levels of the Neandertals that have attracted attention, with implications of a competitive disadvantage relative to early modern humans. However, such assessments are dependent upon the accuracy of absolute body mass estimations and climate variables, as well as secure sex attribution. The last is frequently ambiguous, especially for Middle Paleolithic and EUP fossils given their dearth of diagnostic pelvic remains. The second has either been approximated for Europe from the Stage 3 Project (Barron et al., 2003; Aiello and Wheeler, 2003) or using global Late Pleistocene climate reconstructions with little attention to in situ climatic indicators (Froehle and Churchill, 2009). And the first requires that reliable means are available for consistent estimation (Auerbach and Ruff, 2004), something that is uncertain for many pre-MUP humans (Trinkaus, 2011a; Trinkaus and Ruff, 2012).

A reassessment of the relevant variables for the maximum number of sufficiently preserved specimens indicates that some Western European male Neandertals likely had elevated DEE levels, but the pattern does not apply to warmer climate males (Figure 12.2). Among “cold” climate remains, the Neandertal males are at the upper limits of the EUP male distribution, as is the one “cold” climate Neandertal female (La Ferrassie 2); this may relate to the thermoregulatory demands of cooler MIS 4– climatic zones in the context of evolving cultural thermal buffering (Aiello and Wheeler, 2003; see below). A sample of probable “temperate” Neandertal females also has relatively high estimated DEE levels. However, the

“temperate” Neandertal males are below the “temperate” EUP males. The few available MPMH specimens providing DEE estimates have among the lower values of these Late Pleistocene humans, for both males (3174 ± 68 kcal/d, $N=4$) and one female (2335 kcal/d). To the extent that these values reflect energy costs among these Late Pleistocene people, they do not provide a large or consistent difference across the two Neandertal and Upper Paleolithic samples.

It has also been suggested (Weaver and Steudel-Numbers, 2005) that the early modern humans would have had more efficient locomotion given their generally longer legs. Indeed, early modern humans, and especially males (or probable males), had leg lengths at or above the upper end of the sex-specific late archaic range of variation (Shang and Trinkaus, 2010: 77), and longer legs should confer an energetic advantage, all else being equal (Pontzer, 2007). However, particularly in the colder climates of Eurasia, but also in more temperate zones, those longer limbs engendered a thermal cost (Trinkaus, 1981; Ruff, 1994), such that the net difference in energetic costs (assuming similar day ranges) would have been small (Maki and Pontzer, 2008).

The longer legs would only have conferred an energetic advantage should the early modern humans have had substantially better thermal protection during locomotion. There is no evidence for such a difference in thermal protection during the Middle Paleolithic, but there are suggestions for improved clothing in the IUP and EUP (d’Errico et al., 2003, 2012; Trinkaus and Shang, 2008; Kuhn et al., 2009), including a possible eyed-needle in the EUP (Golovanova et al., 2010); there is also anatomical evidence of more habitual use of protective footwear in the EUP and especially the MUP (Trinkaus, 2005a; Trinkaus and Shang, 2008). Secure evidence for clothing only appears in the earlier MUP (Abramova, 1995; Adovasio et al., 1996; Musil, 1997; Bader, 1998; Soffer et al., 2000; Trinkaus, 2005a), with occasional evidence for eyed-needles during the MUP (Stordeur-Yedid, 1979; Soffer et al., 2000). In any case, it is unlikely that any of these human groups survived in colder Eurasian climatic zones without thermally effective clothing (Maki and Pontzer, 2008; Sørensen, 2009).

Consequently, given these considerations, it is difficult to argue for significant contrasts in DEE between late archaic and early modern humans. All of them are likely to have had high DEE levels compared to Holocene humans (cf. Stein et al., 1988; Steegmann et al., 2002; Snodgrass et al., 2006). In addition, possible differences in locomotor efficiency engendered thermal costs are likely to have reduced any energetic advantages of longer limbs.

Ultimately, these energetic issues may be of relevance to the emergence of modern humans, if they had bearing on the demographics of late archaic versus early modern humans. It is often assumed (e.g., Froehle and Churchill, 2009) that lower energy throughput will provide a reproductive advantage, although cross-species comparisons indicate that species with higher DEE often have higher net reproduction (Pontzer and Kalimar, 2009).

Subsistence Issues

Concerns with energetics must also address possible differences in subsistence effectiveness. There were improvements in projectile technology, appearing sporadically in the South African MSA (Villa and Soriano, 2010; Lombard and Phillipson, 2010) and then more consistently in IUP of Western Eurasia (Volkman and Kaufman, 1983; Plisson and Schmider, 1990; Shea, 2006; Shea and Sisk, 2010), as well as in the subsequent EUP. They may imply greater efficiency in at least animal protein acquisition. However, the initial improvements in hunting weaponry in Europe (Shea, 2006) are late archaic human associated (Lévêque and Vandermeersch, 1980; Bailey and Hublin, 2004; Harvati et al., 2003) and appear prior to the documented presence of Upper Paleolithic modern humans in Southwest Asia (Trinkaus and Buzhilova, 2012;

Trinkaus, in press a). Moreover, where associated faunal remains have been appropriately analyzed through the transition (Stiner, 1994; Marean and Kim, 1998; Grayson and Delpech 2003; Bar-Yosef, 2004; Speth and Clark, 2006; Adler et al., 2006), there are no meaningful differences in macromammal faunal acquisition and processing until after the EUP.

As noted above, human stable isotope data and small vertebrate exploitation suggest some broadening of the protein sources with the EUP and into the MUP (but see Hardy and Moncel, 2011), but those data are best interpreted as indicating increased population pressure on large mammal resources and not necessarily any improvement in food acquisition (Stiner et al., 1999; Richards and Trinkaus, 2009). If differential energetics played a role in this, it may well have been at a very modest level.

Related but rare subsistence data come from evidence for plant processing, cooking, and consumption, among both Middle Paleolithic Neandertals (Lev et al., 2005; Henry et al., 2011) and MUP modern humans (Revedin et al., 2010). Such plant foods should have been widespread, even in glacial Europe (Hardy, 2010), and they would be combined with the animal protein reflected in the zooarcheological assemblages and stable isotope data to provide the dietary balance needed in both human groups (cf. Cordain et al., 2000).

The Possible Role of Noses

Curiously and possibly related, there was a decrease in nasal aperture breadth between the Middle and Upper Paleolithic samples, as opposed to between late archaic and early modern humans (Wu and Poirier, 1995; Franciscus, 2003; Doboş et al., 2010). This change may reflect respiratory physiological shifts, related to activity levels in the context of other aspects of respiratory physiology (cf. Trinkaus, 1987; Dean, 1988; Franciscus and Trinkaus, 1988). However, nasal aperture dimensions are related to a complex mix of facial prognathism, thermoregulation, and respiratory physiology (Holton and Franciscus, 2008). Yet, given that the shift in nasal breadth occurred consistently across the Old World only ~40–50 ka BP, after the modest reduction in prognathism of the Neandertals and the continued reduction of African late archaic human and MPMH faces (Trinkaus, 2003), the nasal breadth decrease may relate to activity-related respiratory physiology. If so, it is not clear how changing nasal dimensions would interrelate with the apparent lack of a consistent change in DEE values or leg strength.

Manipulation

Archeological Context

Despite isolated and temporary changes in projectile weaponry within the MSA of Southern Africa (Shea, 2006; Lombard and Phillipson, 2010; Villa and Soriano, 2010), the basic technology of the Middle Paleolithic/MSA appears to have been consistent across at least the western Old World in terms of stone tool manufacture, hafting, and utilization. In Eastern Asia, the same time period witnessed a continuation of a lithic technology more akin to the Lower Paleolithic (Gao and Norton, 2002). A series of changes then took place, most evident in projectile weaponry, with the IUP of Western Eurasia, which continued to become elaborated through the EUP and the MUP. In particular, there was a marked shift from flake-based lithic assemblages to ones based on blade/bladelet production, and there was the marked elaboration of organic technologies from the IUP through the EUP and MUP (Bar-Yosef and Zilhão, 2006; Teyssandier et al., 2010; d'Errico et al., 2003, 2012).

Middle Paleolithic *sensu lato* technology was associated with archaic humans across most of Eurasia. However, it was made by early modern humans in Eastern Africa and Southwestern Asia (Shea, 2008; Hovers, 2009), and early modern humans in Southeastern

Asia occurred well before the Upper Paleolithic (Liu et al., 2010a; Demeter et al., 2012). It was also made by archaic humans in Africa. The initial stages of the Upper Paleolithic were the product of late archaic humans across Europe, but its manufacturers in Southwestern Asia are unknown. The MUP was the product of modern humans, as were the more recent phases of the EUP (Bailey et al., 2009). However, there are *no* diagnostic human remains directly associated with the technological developments of the earliest phases of the EUP (such as the proto-Aurignacian and Aurignacian I of Europe), in Europe or elsewhere (Oase and Tianyuan come closest but are not associated with technocomplexes [Zilhão et al., 2007; Shang and Trinkaus, 2010], the Southwest Asian Ksar Akil 1 early modern human may date to this period, but its precise age within the EUP is unknown (Bergman and Stringer, 1989), and there are uncertainties as whether Kent's Cavern 4 is earlier than Oase 1 and 2 [Higham et al., 2011; White and Pettitt, 2012]).

Upper Limb Hypertrophy

In this Paleolithic framework, there were a number of changes in human manipulative anatomy that indicate a decrease in the use of the human anatomy to accomplish manipulative tasks. While some of the shifts are largely or exclusively the result of plasticity, others appear to be developmentally stable and hence of uncertain short-term adaptive significance. All of the contrasts, however, occurred within the context of no discernible change in manipulative capabilities. Moreover, few if any of the changes are absolute between late archaic and early modern humans, given variation in both samples (cf. Hambücker, 1993; Trinkaus, 2006d, 2007; Pearson et al., 2008a; Shang and Trinkaus, 2010; Walker et al., 2011a).

These changes include a general reduction of muscle moment arms and/or muscular attachment hypertrophy between late archaic and early modern humans, as well as in levels of anterior dental attrition. The upper limb shifts are not, however, associated with any significant changes in diaphyseal rigidity, of the clavicle, the long bones, the metacarpals, or the phalanges (Trinkaus, 2006d).

A series of proportional differences in the upper limb between late archaic and early modern humans appear to indicate greater effective mechanical advantages (EMAs) for the former, particularly in limb postures involving power rather than speed (Fischer, 1906; Trinkaus, 1983c; Trinkaus and Churchill, 1988; Villemeur, 1994; Churchill and Rhodes, 2006; Maki and Trinkaus, 2011). These proportional contrasts involve, for late archaic humans, long clavicles, wide scapulae, long olecranons, more distal and more medial radial tuberosities, pronounced radial lateral curvature, palmar projection of the hamulus, pisiform bone and trapezoid tuberosity, opponens flanges on the first metacarpals, and length proportions of the pollical phalanges (Figure 12.3). For only three of these (elbow anatomy, metacarpal 1 opponens flanges, and pollical phalangeal flexion) have both the power and load arms been taken into account. The overall impression is nonetheless one of late archaic human upper limbs focused more on power than those of early modern humans. Moreover, many of these contrasts, especially those of the forearm and hand, appeared relatively early during childhood (Vlček, 1975; Heim, 1982b; Tillier, 1999; Trinkaus et al., 2002b).

Yet, it remains to be assessed to what degree the reduced EMA for early modern humans would have been important in the context of differential muscle development. Several of these contrasts may have reduced contractile forces needed in antagonists and synergists for joint stabilization, thereby reducing joint reaction forces during vigorous manipulation. At least one of the primary manipulation articulations, the first trapeziometacarpal one, was palmarly elongated (and hence “flatter”) in most, but not all, late archaic humans (Trinkaus, 1989b; Niewoehner, 2001; Walker et al., 2011a), which may thereby have reduced joint

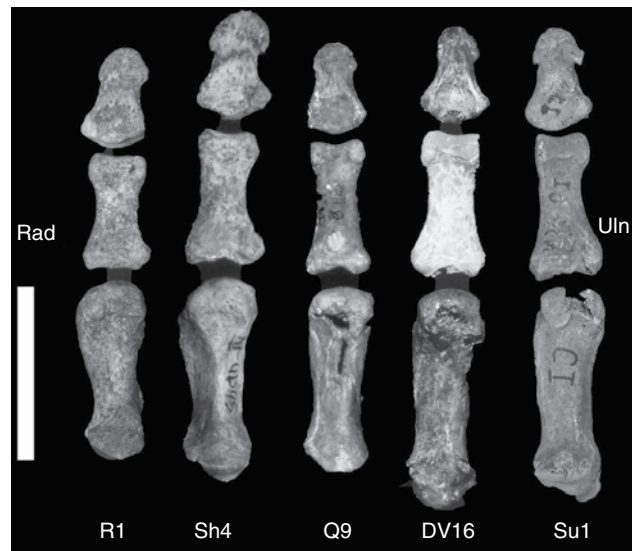


Figure 12.3. Palmar views of Late Pleistocene pollical metacarpals and phalanges, reversed as needed to all appear as left thumbs. Neandertals: Regourdou 1 (R1) and Shanidar 4 (Sh4); MPMH: Qafzeh 9 (Q9); MUP: Dolni Věstonice 16 (DV16) and Sunghir 1 (Su1). Rad: radial; Uln: ulnar. Scale: 5 cm. Note Neandertal opponens pollicis flanges on the metacarpals and their subequal lengths of the pollical phalanges, which translate into greater EMA in power grips. The late archaic humans also have more pronounced ulnar deviation of the distal phalanges and larger apical tuberosities.

pressure. Most Neandertal scapular glenoid fossae were relatively narrow compared to those of MUP and recent humans (Churchill and Trinkaus, 1990; Trinkaus, 2006d; Churchill and Rhodes, 2009), although only two of the three known EUP individuals with a glenoid fossa exhibit the wider configuration (Crevecoeur, 2008; Trinkaus, 2008b; Shang and Trinkaus, 2010) (none of the MPMH ones are sufficiently preserved). The narrower glenoid fossae of most Neandertals and of the EUP Muierii 1 have been seen to indicate less throwing behavior (Churchill and Trinkaus, 1990; Trinkaus, 2008b; Churchill and Rhodes, 2009; but see Maki, 2013), and they would also have reduced the ability of the articulation to resist joint reaction forces. In the case of the opponens pollicis insertion, the flanges for the muscle in most Neandertals and some early modern humans may not reflect muscle hypertrophy, and the changes in EMA are principally between Middle Paleolithic and MUP humans (Maki and Trinkaus, 2011). And any changes in elbow EMA are likely to have had little effect on power or speed for one of the more relevant activities, projectile throwing (Maki, 2013).

There was also a reduction in muscle attachment hypertrophy in the upper limbs of early modern humans, including the MPMH. This is reflected in scapular surface area, thoraco-humeral insertion tuberosities on the proximal humerus (especially of pectoralis major), distal ulnar pronator quadratus crests, palmar carpal tuberosity size (in addition to palmar projection), and opponens muscle insertions on both the pollex and the fifth metacarpal (Trinkaus, 1983c, 2006d; Hambücker, 1993; Churchill, 1994; Doboş et al., 2010). If these late archaic human skeletal attachment areas reflect muscle hypertrophy, then it is likely that their antagonists and synergists were similarly enlarged. However, the combination of changes in both muscle EMA and apparent muscular hypertrophy between late archaic and early modern human upper limbs presents a persistent paradox, in that increases in EMA should obviate the need for muscular hypertrophy.

These muscle-related shifts are combined with a generalized reduction in distal phalangeal tuberosity size between late archaic and early modern humans. However, the IUP Saint-Césaire 1 and the EUP Tianyuan 1 exhibit the archaic *Homo* pattern, the MPMH have reduced tuberosities, and at least one Neandertal (Palomas 96) has modest tuberosities (Trinkaus, 1983c, 2006d; Crevecoeur, 2002; Shang and Trinkaus, 2010; Walker et al., 2011b). Since it reflects ungual pad size (Mittra et al., 2007), it may indicate habitual load levels on fingers. Yet, the contrasts are evident relatively early in development (Heim, 1982b).

These upper limb considerations are based principally on the remains from Western Eurasia, plus inferences from Nazlet Khater 2 and Tianyuan 1. The few sub-Saharan African MSA upper limbs indicate an East-South African contrast. The Omo-Kibish postcrania are relatively gracile, similar to the Southwest Asian MPMH (Pearson et al., 2008a,b). The South African MSA postcrania are either uninformative or archaic (Grine and Klein, 1993; Churchill et al., 1996; Pearson and Grine, 1997).

Anterior Dental Attrition

There was a shift in the level of anterior dental attrition, apparently from non-dietary use of the teeth (Figure 12.4). There is an average decrease in the summed volume of the anterior dentition in early modern humans, both Middle and earlier Upper Paleolithic, reflected in both crown diameters and a reduction in shoveling (Stefan and Trinkaus, 1998; Bailey, 2006). Yet, for a given degree of postcanine wear, the early modern humans exhibit less anterior dental attrition. This is apparent in both younger and older adults with sufficient occlusal wear to reveal the pattern. The pattern of beveling of the anterior teeth, however, is similar across the samples, if more pronounced among the Neandertals (Ungar et al., 1997). The one African Middle Paleolithic/MSA dentition with anterior and posterior teeth (Témara 1) is insufficiently worn to indicate their relative anterior wear (Ménard, 1998).

Summary

Therefore, there was a generalized reduction in EMA and muscle hypertrophy of the upper limb between late archaic and early modern humans. This shift is pervasive from the proximal clavicle to the terminal phalanges. It is joined by altered anterior dental attrition patterns. Curiously, the paleobiological shift took place initially within the Middle Paleolithic, in the context of little discernible functionally relevant contrasts in technology. Subsequently, the one IUP Neandertal with dental arcades and postcrania presents a distinctly archaic pattern (Trinkaus et al., 1999; Crevecoeur, 2002). The few EUP postcrania (Mladeč, Muierii, Nazlet Khater, Tianyuan) are more modern but present a mosaic of “modern” and “archaic” upper limb features. Nonetheless, most of the sufficiently complete EUP dentitions have the reduced anterior wear of early modern humans (Trinkaus et al., 2006a; Frayer et al., 2006; Crevecoeur, 2008; Shang and Trinkaus, 2010; Doboş et al., 2010). There is therefore a fit between paleobiologically implied manipulative behavior and the associated technologies if one considers principally the Middle Paleolithic archaic humans and the MUP modern humans. The MPMH stand out as an exception. Given the technological changes between the Middle Paleolithic and the IUP, one might also expect more paleobiological contrast between Saint-Césaire 1 and the Middle Paleolithic archaic humans.

Stress and Survival

These various paleobiological issues relate to an assessment of levels of stress and survival. In such considerations, beyond diagnosing lesions on human remains (nonetheless a first step), there has been a shift from seeing the lesions in terms of “stress” to one more concerned

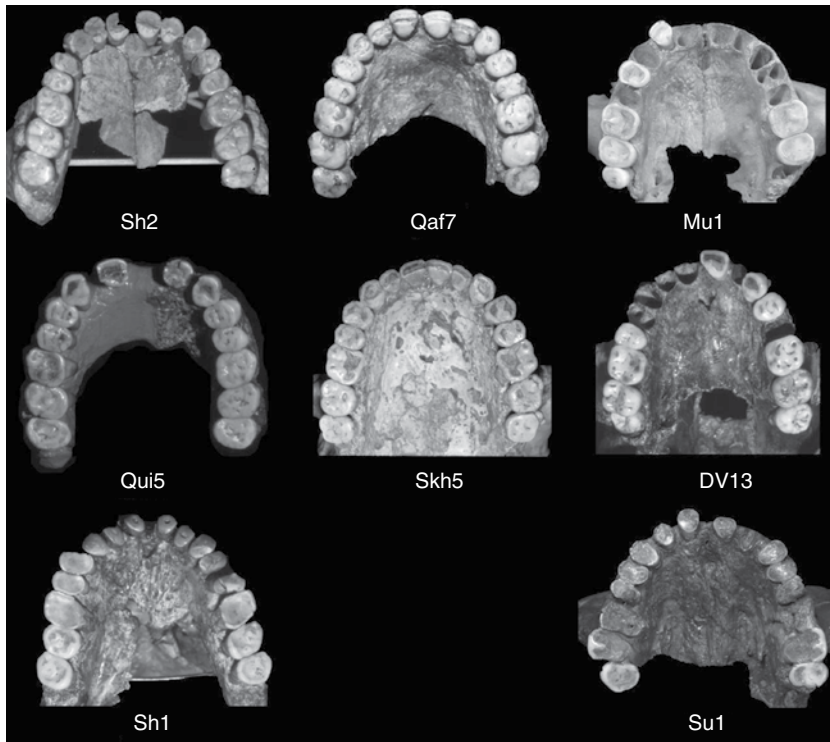


Figure 12.4. Occlusal views of maxillary dentitions for late archaic humans (left), Middle Paleolithic modern humans (center), and earlier Upper Paleolithic humans (right). Sh2: Shanidar 2; Qui5: La Quina 5; Sh1: Shanidar 1; Qaf 7: Qafzeh 7; Skh5: Skhül 5; Mu1: Muierii 1; DV13: Dolní Věstonice 13; Su1: Sunghir 1. Shanidar 1 and Sunghir 1 are older adults with substantial occlusal wear; the remainder are younger adults, in the third or fourth decade postnatal. Approximately to scale.

with the balance between “stress” and “survival.” Indeed, with one exception (Trinkaus and Buzhilova, 2012), all of the indicators of stress among Late Pleistocene humans are observable only as a result of the individual’s survival of the insult.

Developmental Stress Indications

Among systemic, non-specific stress indicators, the most common lesions are dental enamel hypoplasias (DEH). Although there are many ultimate causes of DEH (cf. Goodman and Rose, 1990), it is likely that nutritional stress was the predominant cause in the Late Pleistocene. In only a few cases, in which there is evidence of serious growth alteration (e.g., Dolní Věstonice 15 and Sunghir 3), the DEH may be due to other systemic stresses (Buzhilova, 2000; Trinkaus et al., 2006b; Guatelli-Steinberg et al., 2011). In general, Neandertals exhibit a high frequency of DEH (Ogilvie et al., 1989; Brennan, 1991; Skinner, 1996), a level nonetheless matched by some recent human samples (Guatelli-Steinberg et al., 2004). The level among MPMH, however, is exceptionally low (Skinner, 1996; Tillier et al., 2004; Trinkaus, personal observation), and even the hydrocephalic Qafzeh 12 lacks them (Tillier, 1999). The DEH level remains relatively low among EUP modern humans (Brennan, 1991; Skinner, 1996; Teschler-Nicola et al., 2006; Doboş et al., 2010). The incidence increases modestly among MUP modern humans, but it does not appear to reach the levels seen in the late archaic humans (Brennan, 1991; Buzhilova, 2000; Trinkaus et al., 2006b).

Given that DEH represents both a disruption of amelogenesis and survival of the insult (Hillson and Bond, 1997), it is not clear whether the differences across these Late Pleistocene samples represent differential stress and/or survival levels; given similarities of subsistence among the Middle Paleolithic humans, the Neandertal-MPMH difference may well be due to differential levels of stress. If the inference of increased population pressure on resources with the EUP holds, then the decreased level of DEH in the EUP and into the MUP may involve some differential survival.

At the same time, the Neandertals exhibit a pattern of increasing incidence of DEH with the later-forming molars, from the dm2 to the M3 (Ogilvie et al., 1989), teeth that should have similar susceptibilities given morphological similarities (Hillson and Bond, 1997). This pattern appears to be absent among early modern humans (Brennan, 1991; Trinkaus et al., 2006b). There are two interpretations of this pattern, affecting teeth that calcified from in utero through the first decade postnatal. It could indicate increasing stress levels as the individuals became independent of maternal nutritional buffering, and/or it could indicate persistently high levels of stress associated with increased survival at older developmental ages. Either scenario implies substantial uncertainty of resources, assuming that the DEH was principally secondary to nutritional scarcity.

Trauma

The Neandertals have been noted for their high level of antemortem trauma, ranging from minor scalp wounds to serious craniofacial or appendicular injuries resulting in partial loss of function (Trinkaus, 1983c; Berger and Trinkaus, 1995; Zollikofer et al., 2002; Smith et al., 2006). To the healed subperiosteal lesions and fractures can be added cases of marked osteoarthritis, which deviate from normal patterns of degeneration and are probably posttraumatic (Trinkaus, 1983c, 1985; Dawson and Trinkaus, 1997). When both forms of evidence for Neandertal antemortem trauma are combined, there is hardly a reasonably complete adult partial skeleton among them without at least one lesion. A similar range of traumatic injuries characterizes early modern humans (Tillier, 1999; Teschler-Nicola et al., 2006; Trinkaus et al., 2006b), although it is possible to find MUP individuals without evidence of antemortem trauma. It is not possible to determine directly whether the apparently higher incidence of trauma among the late archaic humans reflects elevated risk, higher survival, or both. It is not due to differential longevity, given the similar proportions of older versus younger adults in the samples (see below). Given that the social mechanisms for survival are not likely to have decreased with early modern humans, it is probable that the shift reflects a reduction in risk.

It has also been noted that Neandertals exhibit primarily upper body trauma, with an absence of serious lower limb injuries (Berger and Trinkaus, 1995). This was originally attributed principally to their Middle Paleolithic weaponry, which would have required close encounters with prey, but it was also noted that it may reflect their need for continued mobility (Berger and Trinkaus, 1995). Since then, it has become apparent that early modern human trauma, both Middle and earlier Upper Paleolithic, is also predominantly on the head and upper limb (Trinkaus, 2012), and as noted above, healed debilitating lower limb injuries are unknown prior to the terminal Pleistocene. This observation indicates that the differential incidence of upper body trauma among the Neandertals, and early modern humans, is most likely a consequence of reduced lower limb injury survival, across all of these Late Pleistocene human populations.

It should be mentioned that during this time period there are only three cases of injuries that were probably inflicted by other individuals, accidentally or intentionally. They include the intercostal puncture of the Middle Paleolithic Shanidar 3, a frontal squamous incision

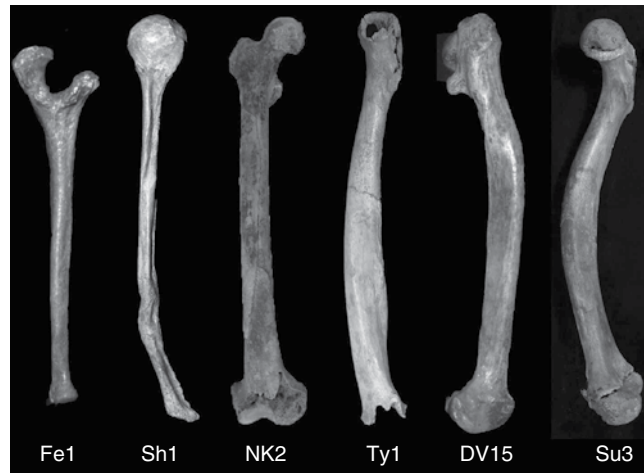


Figure 12.5. Views of abnormal long bones of Late Pleistocene humans. Fe1: Feldhofer 1 left ulna, which sustained a deforming proximal fracture prior to maturity, sufficient to produce marked humeral diaphyseal asymmetry (Trinkaus et al., 1994; Smith et al., 2006). Sh1: Shanidar 1 right humerus (the head is plaster), with atrophy or hypotrophy, multiple fractures, and a pseudoarthrosis or amputation at the olecranon fossa level (Trinkaus, 1983c). Nazlet Khater 2 right femur, which is too short, has marked anterior curvature and a high neck-shaft angle, yet is unusually robust (Crevecoeur, 2008). Tianyuan 1 right femur with a distal diaphyseal flange parting the linea aspera and midshaft cortical remodeling (Shang and Trinkaus, 2010). Dolní Věstonice 15 right femur, with low neck-shaft angle and marked proximal diaphyseal bowing (associated with small body size plus right humeral and left forearm diaphyseal deformities) (Trinkaus et al., 2006b). Su3: Sunghir 3 juvenile right femur with bilaterally symmetrical, marked anterior bowing (Buzhilova, 2000; Mednikova, 2000; Formicola and Buzhilova, 2004).

on the IUP Saint-Césaire 1, and an upper thoracic wound on the MUP Sunghir 1 (Trinkaus, 1983c; Zollikofer et al., 2002; Trinkaus and Buzhilova, 2012). Only the last was immediately fatal, and none are likely to have been inflicted by someone unknown to the victim (cf. Trinkaus and Buzhilova, 2012).

Serious Abnormalities

There are also Late Pleistocene cases of serious abnormalities, ones that could have affected survival (Figure 12.5). Among the Neandertals, these cases involve loss of one arm function in Feldhofer 1 and Shanidar 1, probable unilateral loss of vision in Shanidar 1, and degenerative lesions in La Chapelle-aux-Saints 1 (Trinkaus, 1983c, 1985; Dawson and Trinkaus, 1997; Smith et al., 2006). The MPMH Qafzeh 11 and 12 children suffered, respectively, a serious neurocranial compressed fracture and hydrocephalus (Tillier, 1999; Tillier et al., 2001). The EUP Nazlet Khater 2 had underdevelopment of the femora (Crevecoeur, 2008), Tianyuan 1 had abnormalities of the distal femora and proximal tibial diaphyses (Shang and Trinkaus, 2010), and Mladeč 2 had a malformed petrous labyrinth (Teschler-Nicola et al., 2006). In the MUP, there are multiple developmental deformities in Dolní Věstonice 15, abnormal femoral bowing in Sunghir 3, marked upper limb asymmetry in Barma Grande 2, systemic infections in Cro-Magnon 1 and Brno 2, and a mandibular fracture with facial asymmetry in Dolní Věstonice 3 (Dastugue, 1967; Oliva, 1996; Churchill and Formicola, 1997; Formicola and Buzhilova, 2004; Trinkaus et al., 2006b). To these specimens can be added several late Middle

Pleistocene cases, including the porotic hyperostosis of ES-11693, the petrous labyrinthine ossification and porotic hyperostosis of Singa 1, and the massive periodontal lesions of Aubesier 11 (Sporer et al., 1998; Lebel and Trinkaus, 2002; Bräuer et al., 2003).

The high incidence of unusual individuals in the MUP may reflect differential burial (Oliva, 1996; Formicola, 2007; Trinkaus and Buzhilova, 2012), but most of these individuals reflect a substantial level of survival in the face of serious insults, through the Middle and earlier Upper Paleolithic. Indeed, similar survival is evident in the Middle Pleistocene (Kricun et al., 1999; Shang and Trinkaus, 2008; Grada et al., 2009; Wu et al., 2011), and the Late Pleistocene differs principally in more thoroughly documenting it in associated skeletons.

Dento-Alveolar Lesions

Except in cases of total loss of function, dento-alveolar lesions tend to be minor, but nonetheless reflect general health status. Yet dental and alveolar abnormalities, other than those directly associated with occlusal attrition, are rare. Alveolar granulomata occur principally with marked attrition and/or tooth loss, and they are present in only a few individuals (Artenac 1, La Chapelle-aux-Saints 1, La Ferrassie 1, Zhiren 3, Tianyuan 1, Cro-Magnon 1, Dolní Věstonice 16, Sungir 1 and Zhoukoudian 101, of which only Zhiren 3 lacks advanced dental wear and/or unassociated antemortem tooth loss) (Dastugue, 1967; Heim, 1976; Trinkaus, 1985; Trinkaus et al., 2006b; Mann et al., 2007; Shang and Trinkaus, 2010; Lacy et al., 2012). Despite marked occlusal attrition in a number of late archaic and earlier Upper Paleolithic individuals, antemortem tooth loss is relatively rare, with the loss of multiple teeth only known for La Chapelle-aux-Saints 1, Guattari 1, Shanidar 5, and Tianyuan 1 (Sergi, 1974; Trinkaus, 1983c, 1985; Shang and Trinkaus, 2010).

Dental carious lesions are present among both late archaic and early modern humans, but they remain rare. Middle Paleolithic ones (both archaic and modern) are present only in Mediterranean samples (Aubesier, Banyoles, Kebara, Palomas, Qafzeh, and Skhül) plus in southern East Asia (Zhiren) (Trinkaus and Pinilla, 2009; Walker et al., 2010; Lacy et al., 2012). A few additional ones are known from more northern European EUP and MUP specimens (Brennan, 1991; Trinkaus et al., 2006b).

Behavioral versus Anatomical “Modernity”

Even though the focus here is principally on changes in human paleobiology with the emergence of modern human morphology, it should be evident that they took place, to varying degrees, within the context of cultural changes, those normally subsumed within the Middle to Upper Paleolithic transition. These biocultural issues have come into focus as Paleolithic archaeologists and human paleontologists try to establish (or refute) correlations between “anatomical modernity” and “behavioral modernity.”

Technology

The primary technological changes are associated with the emergence of the Upper Paleolithic in mid-MIS 3 (~40–50 ka BP). However, in Eastern Africa, briefly in Southwest Asia, and in southern East Asia, anatomical modernity emerged in a Middle Paleolithic (*sensu lato*) technological context (Shea, 2008; Hovers, 2009; Liu et al., 2010a). The one technological development that has received special attention, projectile weaponry to facilitate predation, developed rapidly through the IUP, the EUP, and into the MUP (Shea, 2006; Villa and Soriano, 2010; Teyssandier et al., 2010; Shea and Sisk, 2010). There are only brief and temporary hints of elaborations earlier in the Southern African MSA (Villa and Soriano,

2010; Lombard and Phillipson, 2010). The improvements in weaponry were already under way among IUP Neandertals, and despite stylistic and lithic reduction differences, the subsequent EUP and MUP changes can be seen largely as continuations of the same trajectory. It is unclear to what extent this projectile elaboration was related to probable population changes and the need for more reliable predation.

Burials

Burial, as a uniquely human and entirely social-psychological phenomenon, has received less attention (but see Pettitt, 2011), since Neandertal burials were recognized as early as 1908 at La Chapelle-aux-Saints (Bouyssonie et al., 1908). Yet formal disposal of the dead is among the most “modern” of Late Pleistocene human cultural developments. The earliest burial is probably the MIS 5 Middle Paleolithic Tabun 1 Neandertal, followed closely in time by the MPMH ones at Qafzeh and Skhul. Then through MIS 4 and early 3, there are a number of late archaic human burials. Few of these Middle Paleolithic burials have yielded unquestionable grave goods or body decoration. Yet the Neandertal burials at La Ferrassie had mortuary architecture (capping stones) and the only distinctive grave goods from the Middle Paleolithic (an engraved bone) (Peyrony, 1934), and Qafzeh 11 was apparently associated with ochre and an antler (Vandermeersch, 1970). Middle Paleolithic/MSA burials are unknown in Africa, as they are in Eurasia east of Uzbekistan.

With the emergence of the Upper Paleolithic, burials initially become scarce. They consist of the IUP Saint-Césaire 1 Neandertal, the Northeast African Nazlet Khater 1-3 early modern humans, and possibly the EUP Tianyuan 1 individual (Lévêque et al., 1993; Vermeersch, 2002; Fernández-Jalvo and Andrews, 2010); the first two had the earliest secure grave goods after those of La Ferrassie (Zilhão and d’Errico, 1999; Vermeersch, 2002). Upper Paleolithic modern human burials are unknown in Western Eurasia prior to the MUP. There is then a marked elaboration of human burials across Eurasia (but nowhere in Africa) during the MUP, with frequent use of pigment (especially red ochre), body decoration, occasional art objects, differential age distributions, gender bias, and differential treatment of the unusual (Verneau, 1906; Klíma, 1995; Oliva, 1996; Bader, 1998; Zilhão, 2005; Formicola, 2007; Norton and Gao, 2008; Trinkaus and Buzhilova, 2012).

It is therefore apparent that the emergence and elaboration through MIS 5–3 of this manifestation of formal disposal of the dead was independent of human anatomical form. Since it depends upon fully “human” social and psychological integration, and is not an isolated cultural “trait” (only the form of the disposal is a cultural “trait”), these patterns establish that the underlying social-psychological foundations were the same across these human groups.

Body Decoration

Humans are unique in routinely using extrasomatic material to alter one’s social persona, and the earliest evidence of this behavior consists of beads of various materials and natural inorganic pigments. In the Middle Paleolithic/MSA, evidence of such body decoration occurs sporadically in time and space in various portions of Western Eurasia and Africa. There is evidence of pigment use among Neandertals in Europe (Peyrony, 1934; Bordes, 1952; Vertés, 1964; d’Errico and Soressi, 2002; Cârciumară and Țuțuianu-Cârciumară, 2009; Zilhão et al., 2010), early modern humans in Southwestern Asia (Hovers et al., 2003; Mayer et al., 2009), and among archaic humans in Southern Africa (Barnham, 2002; Marean et al., 2007). Beads, made of shells or teeth, appear sporadically in Southern and North-western Africa with archaic humans (d’Errico et al., 2005, 2008; Vanhaeren et al., 2006; Bouzouggar et al., 2007), among early modern humans in Southwest Asia (Vanhaeren et al.,

2006; Mayer et al., 2009), and with Neandertals in Europe (Zilhão et al., 2010). In addition, they are evident in European IUP assemblages associated with Neandertals (Taborin, 1990; Granger and Lévêque, 1997) and with undiagnostic human remains in the Southwest Asian IUP (Kuhn et al., 2001, 2009). There is also evidence of the collection of feathers by Neandertals, apparently for body decoration (Peresani et al., 2011). Archeologically visible evidence of Middle Paleolithic body decoration is therefore rare but widespread in the western Old World. It is only in Eastern Eurasia that it has so far eluded detection.

Body decoration becomes more frequent in the EUP (or initial Late Stone Age), at least across Western Eurasia and portions of Africa (Ambrose, 1998; Vanhaeren and d'Errico, 2006), and it becomes common throughout the MUP and across Eurasia (Taborin, 2000; Norton and Gao, 2008). Indeed, some of the most elaborate instances of body decoration in the Paleolithic, involving abundant ochre and beads, derive from MUP burials (e.g., Klima, 1995; Oliva, 1996; Bader, 1998; Vanhaeren and d'Errico, 2002; Norton and Gao, 2008). Something in the complexity of interpersonal or intergroup social relationships changes with the EUP and then the MUP at least in Eurasia, and this may well reflect the ethnic diversification that comes from increasing population size (Vanhaeren and d'Errico, 2006).

Geometric and Representational Art

The oldest secure evidence for representational art, in the form of statuettes, engravings, or parietal art, currently appears only in the middle to later phases of the EUP in a few small regions of Europe (Neugebauer-Maresch, 1999; Holdermann et al., 2001; Clottes, 2001; Conard, 2009); it does not become common or widespread until the MUP (Abramova, 1995; Svoboda et al., 1996; Mussi et al., 2000). However, engraved geometric designs appear earlier. Some of the earlier instances on bone may be incidental to animal processing, but a sufficient number of finely engraved examples are present from Middle Paleolithic/MSA contexts. They occur in late archaic human contexts in East Asia, Europe, and Southwestern Asia (Peyrony, 1934; Davis, 1974; Marshack, 1996; Gao et al., 2004), they are present in Southern Africa with archaic humans (Henshilwood et al., 2002; Texier et al., 2009), and there is evidence of them associated with MPMH in Southwestern Asia (Hovers et al., 1997). Although some present more regular geometric patterns, it is apparent that engraved designs, as with body decoration, occurred rarely and sporadically prior to the Upper Paleolithic. They are associated with all of the morphologically defined human groups, but it is only millennia after the transition to the EUP, and especially in the MUP, that such "art" becomes widespread.

Possibly related to these manifestations of "art" is the occasional collection of fossils in the European Middle Paleolithic (Imbert, 1987; Lhomme and Freniex, 1993), something that does not become common until the MUP (Taborin, 2000; Hladilová, 2005).

Implications

These considerations of various aspects of "behavioral modernity" in the context of "anatomical modernity" should make it apparent that, on a pan-Old World scale prior to the EUP, there is little correlation between human biological form and elaborations of human social, symbolic, and aesthetic qualities. It is only within the EUP (but not at its beginning) and especially within the MUP that there is a qualitative and quantitative jump in these facets of human behavior. As noted above, except for a few late Neandertals in the cul-de-sacs of Western Europe, only early modern humans were around during the time of the later EUP and the MUP. It is therefore likely that these Upper Paleolithic behavioral elaborations, in the regions in which they are apparent, were the results of

cultural evolutionary processes within the earlier Upper Paleolithic and not the spread of modern human biology per se.

Life History Issues

Of direct relevance to paleobiological and behavioral shifts with the emergence of modern humans are life history and demographic issues. In the assessment of baseline life history parameters of late archaic versus early modern humans, the null hypothesis should be that there was little if any difference across the samples, given the close correlation between life history parameters and brain size (Smith, 1991; Smith and Tompkins, 1995). Cranial capacities are insignificantly different across the relevant samples (Neandertals: 1464 ± 181 [16]; MPMH: 1486 ± 98 [8]; EUP: 1456 ± 135 [6]; MUP: 1496 ± 147 [22]; mean \pm standard deviation [N]; ANOVA $P = 0.899$).

Developmental Rates

Ongoing research has increasingly documented differences in the detailed patterns of dental development across Late Pleistocene human samples (Smith et al., 2007, 2010; Bayle et al., 2009, 2010; Guatelli-Steinberg and Reid, 2010), despite considerable variation in recent human samples (Tompkins, 1996a; Reid et al., 2008; Guatelli-Steinberg, 2009), a dearth of detailed data for early modern humans (Bayle et al., 2010), and general similarity of relative dental development at a macroscopic level (Tompkins, 1996b). Moreover, the patterns of variation of the paleontological samples relative to recent humans do not strictly follow a late archaic/early modern human dichotomy (Bayle et al., 2010; Guatelli-Steinberg and Reid, 2010). Yet it is difficult to reach a consensus as to whether there were significant differences in rates of dental development across samples of Late Pleistocene humans (Ramirez Rozzi and Bermúdez de Castro [2004] and Smith et al. [2007, 2010] vs. Guatelli-Steinberg et al. [2005] and Macchiarelli et al. [2006]; cf. Guatelli-Steinberg [2009] and Shackelford et al. [2012]). This is especially true when the levels of individual variation (relevant for small fossil samples) in both relative dental development and dental development versus chronological age in recent humans are taken into account (Tompkins, 1996a; Liversidge, 2003; Guatelli-Steinberg, 2009; Shackelford et al., 2012). Moreover, while there are high-resolution dental developmental data for Middle Paleolithic humans, what is known about earlier Upper Paleolithic modern humans (Tompkins, 1996b; Bayle et al., 2010) suggests a mosaic and non-Holocene pattern among them.

It may be that there were subtle differences between late archaic and early modern humans in dental developmental rates, as suggested by Wolpoff (1979), but they are likely to have remained modest on an overall life history scale. The strong correlations between dental and general somatic growth at high taxonomic levels do not always hold for lower taxonomic levels (Guatelli-Steinberg, 2009), and there is considerable variation among modern humans in the timing of the key developmental parameter, sexual maturity (e.g., Herman-Giddens, 2006; Walker et al., 2006). The suggestions of a slower rate of development among early modern humans may indicate less stressful childhoods among them (Walker et al., 2006), in concordance with the reduction in non-specific stress indicators (see above). But if they are associated with later sexual maturity, that would reduce the abilities of those early modern humans to recover from demographic fluctuations.

It should be noted that the presence or absence of contrasts in overall rates of dental (and by inference somatic) development need not say anything about the relative rates of development (heterochrony) of specific anatomical complexes. Such differences exist (e.g., Maureille and Bar, 1999; Tillier, 1999; Krovitz, 2003; Majó and Tillier, 2003; Ponce de

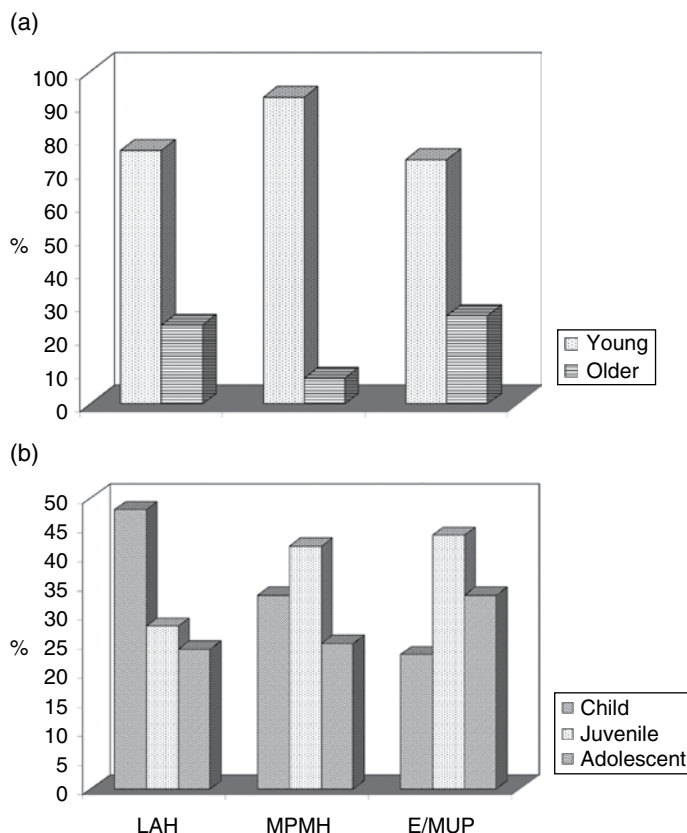


Figure 12.6. Percentages of Late Pleistocene individuals in (a) younger (20–40 years) vs. older (> 40 years) adults, and (b) child (1–5 years), juvenile (6–12 years), and adolescent (12–18 years) age categories for late archaic (LAH), Middle Paleolithic modern (MPMH), and pooled Early and Mid Upper Paleolithic modern humans (E/MUP). Adult sample sizes: LAH: 59; MPMH: 12; E/MUP: 49. Immature sample sizes: LAH: 50; MPMH: 12; E/MUP: 39. Only associated remains or maxillae/mandibles with age indications are included. Infants (< 1 year) are not included given their poor preservation.

León and Zollikofer, 2001; Ponce de León et al., 2008) and are to be expected given the contrasts in adult morphology.

Mortality Patterns

At the other end of the life cycle, it has been noted that Neandertal remains, however grouped, exhibit a dearth of older individuals (20–25%) compared to late Holocene archaeological (31–53%) and especially ethnographic (52–80%) samples (Trinkaus, 1995, 2011b). Not including isolated teeth or isolated postcrania, 23.7% (N=59) of the available late archaic humans are likely to have passed ~40 years postnatal (Figure 12.6a). This pattern was taken to indicate considerable demographic stress and instability (Trinkaus, 1995). However, this adult mortality pattern also characterizes similarly ageable early modern human samples (Trinkaus, 2011b; contra Caspari and Lee, 2004). Among MPMH, only one of the adults (7.7%, N=13) is likely to have passed the fourth decade, and a similarly

depressed pattern is evident among EUP humans (11.1%, $N=9$). In the MUP, the percentage of older adults is slightly higher than in the Middle Paleolithic samples (30.0%, $N=40$) but is at the low end of the late Holocene expectations for older adult survival (pooling the EUP and MUP samples provides 26.5% older adults [$N=49$]). Whatever the demographic (low life expectancy and group instability) and/or behavioral (mobility with old age abandonment) reasons there might have been for these distributions of adult mortality, there is little difference across these Late Pleistocene samples.

Although many of the specimens are grouped into older versus younger adult based on dental attrition in the three relevant studies (Trinkaus, 1995, 2011b; Caspari and Lee, 2004), the similar mortality profiles are not likely to be affected by the tendency of Neandertals to have thinner dental enamel (Zilberman and Smith, 1992; Olejniczak et al., 2008). There is a close correspondence between inferred dental and skeletal ages in both Neandertals and early modern humans, the level of resolution of dental wear employed is relatively gross, and marginal individuals were shifted into the older age category (cf. Trinkaus, 2011b).

Curiously, while the Neandertal postinfantile immature mortality pattern closely approximates what would be expected for recent human populations without medical intervention, the MPMH and earlier Upper Paleolithic patterns are anomalous (Figure 12.6b; see Trinkaus, 1995). The first has relatively high childhood mortality, combined with reduced juvenile and adolescent mortality. The latter samples have especially high juvenile mortality and still high adolescent mortality. In the earlier Upper Paleolithic sample, the higher frequency of adolescents may be due to a burial bias toward socially mature individuals (Zilhão, 2005), but that does not explain the abundance of juveniles in the samples.

Summary

Therefore, although subtle differences in rates of development or adult survival may have existed across these samples, the currently available data are unable to reject a null hypothesis of similarity. The lack of a contrast in adult mortality patterns across these Late Pleistocene samples, given the multiple lines of evidence implying population expansion with the earlier Upper Paleolithic (see above), suggests that any demographic differences may relate more to fertility and/or immature mortality than overall longevity and/or population stability. Yet the available immature mortality data provide a mixed picture.

Discussion

It was noted above that early modern humans succeeded late archaic ones across the Old World in an evolutionary relatively short period of time, and from this observation emerged the inference that there was something behaviorally, and hence adaptively, more effective about those early modern humans. In light of the considerations above regarding a variety of aspects of Late Pleistocene human paleobiology, population patterns, and material culture, the question remains as to what features or complexes clearly changed with the appearance, dispersal, and eventual domination of derived modern human biology.

Although the process occurred relatively rapidly in macroevolutionary terms, current chronology and geographical patterning indicates that this was, in microevolutionary terms, a long and complex process. Derived modern human anatomy appears >150 ka BP but does not become the sole human morphological pattern until <35 ka BP. It is $>50,000$ years between the appearance of modern human anatomy and its first major geographic dispersal. It is then another 60,000 years before it becomes the sole pattern. And in at least one region it is replaced by an archaic morphology, not to reappear for another 50,000 years. This geochronological

pattern will be modified with additional discoveries and dating, but it is sufficient to indicate that the expansion of the “modern human range” into the “archaic human range” occurred in fits and starts with regressions over tens of millennia, and it may well have been heavily influenced by shifting ecozones through Late Pleistocene climatic cycles.

The final human biological transition, although heavily based on data from Western Eurasia, is increasingly showing little documentable change in a variety of paleobiological and material culture aspects. These involve locomotor levels and patterns, developmental rates, energetics, mortality patterns, distributions of trauma, survival of serious impairments, and an emphasis on mobility. To these are added macromammal predation and associated weaponry plus socially relevant burials, body decoration, and design generation. The more impressive cultural developments commonly associated with modern humans and the Upper Paleolithic, such as representational art and elaborate organic technologies, either occur after the transition or are associated with the final stages of modern human expansion into the peripheral cul-de-sacs of the Old World.

The primary paleobiological changes evident between late archaic and early modern humans involve reductions in upper limb hypertrophy, non-dietary use of the anterior dentition, and (probably) levels of stress during life. There are also suggestions of increasing reliance on smaller-package vertebrate resources, probably as part of increased population sizes. Most of these changes are associated with the shift to modern human anatomy within the earlier Upper Paleolithic, but the ones related to manipulation and general stress levels also occur between the two groups within the Middle Paleolithic.

The paleobiological contrasts between late archaic and early modern humans within the Middle Paleolithic are enigmatic, given the similarities in most aspects of their biology (as opposed to morphology) and associated archeological records. The shifts with the final dispersals of modern humans, < 50 ka BP, may well be related to increases in population size and related consequences in subsistence behavior, technology, social patterns, levels of symbolic communication, and levels of stress. It appears contradicted only by the persistent absence of older adults in the paleontological samples. This inference also, of course, begs the question of what triggered the population expansion and what evolutionary forces resulted in the differential expansion of those anatomically modern human populations.

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Index

- Acculturation models, 242
- Activity energy expenditure
 - cost of transport and, 298
 - diet breadth and, 299
 - efficiency and, 297
 - factors influencing, 297
 - foraging habits, 296–97
 - fossil record and, 297
 - Homo heidelbergensis* and, 298
 - issues surrounding, 296
 - limb length and, 297–98
 - Neandertal and modern
 - human, 298–99
 - running and, 299
- La Adam, 174t, 176f, 187
- Adaptive introgression, 360, 382n10
- Aduma, 18
- Africa
 - Aduma, 18
 - Baringo Kapthurin and, 10–11
 - Berg Aukas and, 11
 - blades in, 345
 - Bodo and, 8–9
 - Border Cave, 20
 - Bräuer's grades of, 4f
 - climatic background regarding, 24
 - consensus models of hominin evolution in,
 - 3–5, 3f, 4f
 - consensus points about, 322–23
 - cranial evolution, sequence of, in, 25, 26f
 - cranial variation and
 - higher phenotypic variation, 328–29, 328f
 - phenotypic variation and distance from
 - Africa, 329
 - Dar-es-Soltane II and, 22–23
 - earliest modern *Homo sapiens* in, 15–20, 17f
 - East Asian features rare or absent in
 - populations of
 - agenesis and, 110
 - extrasutural bone at lambda and, 111
 - frontal boss and, 111–12
 - gabled vault and, 110–11
 - mandibular torus and, 110
 - pinched nose and, 110
 - shovel-shaped incisors and, 111
 - Eliye Springs and, 13
 - Eyasi remains and, 14
 - Fish Hoek 1, 23
 - Florisbad and, 12–13
 - fossil record to mid 1980s, 3–5
 - genetics
 - cranial variation and, 328–29, 328f
 - MSA Africans and, 345–47
 - genetics variation
 - declines with distance from
 - Africa, 325
 - higher in, 324–25
 - genomics, xix–xx, 345–47
 - Haua Fteah and, 23
 - Herto, 17–18, 17f
 - Hoedjiespunt and, 11–12
 - Hofmeyr and, 20–21
 - hominin evolution in, 3–5, 3f, 4f
 - hominins from Late MSA or Early
 - LSA, 20–23
 - Homo erectus* in, 6–8
 - Jebel Irhoud remains and, 15
 - Kabwe and, 9–10
 - Klasies River, 18–19
 - KNM-ES 999 and, 13–14
 - KNM-ES 3884 and, 13
 - late archaic transition to *Homo sapiens* in,
 - 12–15
 - migration out of, xv–xvi
 - modern and African anatomy
 - and, 363–65, 365f

Africa (*cont'd*)

MSA

- dating in, 2–3

- genetic diversity within, 345–47

- mt DNA and, 1–2

- Mumbwa and, 21

- Nazlet Khater and, 22

- Ndutu and, 10

- Ngaloba cranium and, 14

- Omo I, 15–16

- Omo II, 14–15

Out-of-Africa Model

- middle ground regarding, 193–94

- recent, 89–90

- Trinkaus and, 193

- what made humans modern and, 347

- overview about, xvii

- Porc-épic and, 21

Recent African Origin model

- origins of, xiii

- verification of, xiv–xv

- regional groups emergence in, 23–24

- Saldanha and, 9

- Singa, 18

- speciation and, 24–26, 26f, 27f

- Stringer's phylogeny and, 27f

- Taramsa Hill and, 22

- transition to archaic *Homo sapiens* in, 8–12

- Tuinplaas, 23

- Weak Garden of Eden Model and, 346

- Y chromosomes and, 2

- Afro-European sapiens hypothesis, 382n3

- Afro-European Sapiens Model, 89

- Agensis, 110

- Amino acid coding sites, 347–48

- Amud, 61, 61f

- age at death, 259t

- Amud 7, 259t

- burials, 72

Anatomical modernity

- African anatomy and, 363–65, 365f

- Assimilation Model and, 364

- behavioral modernity versus

- art, geometric and

- representational, 412

- body decoration, 411–12

- burials, 411

- implications, 412–13

- overview, 410

- technology, 410–11

- cladistic analysis and, 363

- cranium comparisons and, 364, 365f

- early, 365, 367–69

- gracility and, 364–65, 366f, 367f, 368f

- mixture involved in, 369

- no single source of, 363

- overview, 363

- problematic areas regarding, 363

- Ancestry, mixed, 360, 361f

- Andrews, P., 96

- Archaic genomes, xviii

- Archi 1, 259t

- Arcy-sur-Cure, 227–28, 228f

- Art, 412

Asia, East

- archaeological record in, 114–15

- conclusions, 110–14

- Continuity with Hybridization

- Model and, 92

- discussion, 110–14

- features rare or absent in

- African populations

- agenesis and, 110

- extrasutural bone at lambda and, 111

- frontal boss and, 111–12

- gabled vault and, 110–11

- mandibular torus and, 110

- pinched nose and, 110

- shovel-shaped incisors and, 111

- modernity and, 113–14

- morphological features common in other regions and in, 112–14

- mosaics of common features in, 112

- other geographical regions and, 93

- overview about, xvii

- Pope and, 95

- recently discovered fossils from, 97–109

- Chaoxian, 98t, 99f, 104

- Dadong, 99f, 104

- Dali, 98t, 99f, 102–3, 103f, 112

- Huanglong Cave, 98t, 99f, 109

- Jinchuan, 98t, 99f, 109

- Jinniushan, 98t, 99f, 101–2, 102f

- Laishui, 99f, 108

- Liujiang, 98t, 99f, 107–8

- Longlin Cave, 99f, 99t, 108–9

- Maludong, 99f, 99t, 108–9

- Nanjing, 99f, 100–101, 101f

- overview of, 97, 98t, 99f, 99t

- Salkhit, 99f, 99t, 109

- Tianyuan Cave, 98t, 99f, 105, 106f, 107

- Yunxian, 98t, 99–100, 99f

- Zhirendong, 98t, 99f, 104–5, 105f

- river metaphor and, 95

- Schmalzer and, 92

- in situ evolution and, 92

- summary about, 115
- Weidenreich and, 90–92
- Wu and, 92–93
- Asia, West
 - birthing
 - rotational, 53–54
 - Tabun C1 pelvis, 54–55
 - body size and shape
 - European Neandertals and, 49–50
 - faunal record regarding, 51
 - Neandertal thoracic morphology, 51–52
 - stature, 50–51
 - TEE and, 52
 - burial
 - Amud, 72
 - background regarding, 67
 - conclusions about, 74
 - Dederiyeh Cave, 73–74
 - earliest evidence of, 67, 68t, 69t
 - Kebara 2 and, 72–73, 73f
 - Mugharet-es-Skhul, 67, 70, 70f
 - Qafzeh, 70–71
 - Shanidar, 71–72, 75n5
 - Tabun C1, 71
 - conclusions about, 74–75
 - craniofacial form
 - Amud and, 61, 61f
 - chronological variation and, 62
 - Dederiyeh Cave and, 62
 - Kebara 2 and, 61–62, 65
 - Late Pleistocene, 57–59
 - MP, 59–63
 - nasal floor and, 64
 - Shanidar and, 60–61
 - Skhul-Qafzeh and, 57–59, 58f
 - spoken language and, 65
 - Tabun C1 and, 62
 - Tabun C2 and, 62–63, 63f
 - teeth, non-dietary
 - use of, and, 64–65
 - Teshik-Tash and, 60
 - UP and, 63–64
 - Zuttiyeh and, 57, 57f
 - Late Pleistocene, anatomical and taxonomic variability, 46–48
 - locomotion, 52–53
 - manipulation
 - carpometacarpal
 - articulations and, 56
 - conclusions about, 56
 - hand and wrist, 55–56
 - upper limb skeleton and, 55
 - Middle Pleistocene, 48
 - overview about, xvii, 45–46
 - trauma and behavioral inferences
 - Jebel Sahaba and, 65
 - Shanidar and, 66–67
 - Skhul Cave and, 66
 - West-Central Asia, 48–49
- Assemblages. *See* Lithic assemblages, Western Eurasian; Transitional assemblages, Western Eurasian
- Assimilation Model, 89
 - anatomical modernity and, 364
 - Central Europe and, Late Pleistocene, 200–201, 204nn26–27
 - history surrounding, xiv
 - middle ground regarding, 193
 - Pope and, 95
 - Western Eurasia and, 224
- Aurignacian, 177, 178, 196–97
 - burial practices, 238
 - complex, 225
 - dental material regarding, 238
 - early contexts of
 - Bacho Kiro, 232
 - Brassempouy, 233
 - Buran Kaya III, 234
 - Dzeravá Skála, 232
 - La Ferrassie, 233
 - Fontana Nuova di Ragusa, 232–33
 - Fossellone, 232
 - Kostenki 14, 233–34
 - Oblazowa, 234
 - Peștera cu Oase, 234–35, 235f
 - La Quina-Aval, 233, 233f
 - later contexts of
 - Cioclovina Cave, 236–37
 - La Crouzade, 237
 - Görömböly-Tapolca, 237
 - Istállós-kő, 237
 - Mladeč, 235–36, 236f
 - Muierii Cave, 236
 - Les Rois, 237
 - proto- contexts of
 - El Castillo Cave, 232
 - Isturitz, 231
 - Le Piage, 231
 - Riparo Bombrini, 231
 - remains scarcity, 238
- Australasia
 - DiHybrid Model and, 125–26
 - discussion about, 140–42
 - gracility and, 367f
 - overview about, xvii, 123–24
 - replacement models and, 124

Australia

- Birdsell and, 124–25
- Denisova and, 138–39
- Dihybrid Model and, 125–26
- discussion about, 140–42
- genetic evidence concerning, 138–39
- Homo floresiensis* and, 139–40
- Javan ancestry evidence
 - autapomorphic features and, 134–35
 - browridges and, 132
 - conclusions about, 135
 - cranial features and, 131, 132–35
 - cranial vault and, 131
 - facial region and, 131
 - frontal bone and, 132–33
 - nuchal torus and, 133–34
 - occipitals and, 134–35
 - overview, 130–31
 - parietal bones and, 133
- legislation impacting, 123–24
- multiple migrations and
 - bio-culturalist viewpoint, 128, 129
 - migrationist viewpoint, 128–29
 - selectionist viewpoint, 128, 129–30
- Single Population Model and, 128
- Trihybrid Model and, 124–25
- Weidenreich and, 126
- WLH 50 and, 135–38, 136f

Bacho Kiro, 174t, 176f, 187–88,
230–31, 232

Bae, C. J., 97

Bailongdong, 115n1

Baringo Kapthurin, 10–11

Basal metabolic rate (BMR)

- body mass estimates
 - for archaic and early modern humans, 289, 290t, 291t, 292t, 293t
 - climate and, 295–96
 - EUP *Homo sapiens*, 289, 291t
 - female compared with male, 289, 290t, 291t, 292t, 293, 293t, 294f
 - Homo heidelbergensis*, 289, 290t
 - LUP *Homo sapiens*, 289, 292t, 293t
 - Neandertal, 289, 290t
 - PAL and, 296
 - Skhül-Qafzeh *Homo sapiens*, 289, 291t
 - in small-scale societies, 295t
- body size estimates, for archaic and early modern humans, 294f
- DEE and, 288
- defined, 288
- Kleiber equation and, 288–89

Behavioral modernity

- anatomical modernity versus
 - art, geometric and representational, 412
 - body decoration, 411–12
 - burials, 411
 - implications, 412–13
 - overview, 410
 - technology, 410–11
- archaeological evidence, 370–71
- cone of, 372
- as demographic process, 373–77, 374f, 375t
- human revolution and, 371–73
- longevity and, 373–77, 374f, 375t
- Mellars and, 382n16
- oral traditions and, 375–76
- positive feedback and, 375
- process focus regarding, 371–72
- questions surrounding, 370
- repetition and, 376
- resources transfer and, 375–76
- Wobst and, 372

Berg Aukas, 11

Binshof-Speyer

- direct dating and, 192
- incorrect dating and, 177

Bio-culturalist viewpoint, 128, 129

Birdsell, J. B., 124–25

Birthing, in Western Asia, 53–55

- rotational, 53–54

- Tabun C1 pelvis, 54–55

Black, George Murray, 123

Blades, 345

BMR. *See* Basal metabolic rate

Bodo, 8–9

Body decoration, 411–12

Body size

- body mass estimates
 - for archaic and early modern humans, 289, 290t, 291t, 292t, 293t
 - climate and, 295–96
 - EUP *Homo sapiens*, 289, 291t
 - female compared with male, 289, 290t, 291t, 292t, 293, 293t, 294f
 - Homo heidelbergensis*, 289, 290t
 - LUP *Homo sapiens*, 289, 292t, 293t
 - Neandertal, 289, 290t
 - PAL and, 296
 - Skhül-Qafzeh *Homo sapiens*, 289, 291t
 - in small-scale societies, 295t
- DEE and, 288
- estimates, for archaic and early modern humans, 294f
- Kleiber equation and, 288–89

- in Western Asia
 - European Neandertals and, 49–50
 - faunal record regarding, 51
 - Neandertal thoracic morphology, 51–52
 - stature, 50–51
 - TEE and, 52
- Bohunician, 203n21, 241
- Border Cave, xiv
 - hominin fossils from, 20
- Bordu Mare, 174t, 176f, 187
- Bottlenecks, in Late Pleistocene, 340–41
- Boule, Marcellin, 151
- Branching population model, 342–43
- Brassempouy, 233
- Bräuer's grades of *Homo sapiens*, 4f
- Brno-Franzcouska, 175t, 176f, 190
- Brown, P., 95–96
- Browridges, 132
- Buran Kaya III, 234
- Burial
 - Aurignacian practices of, 238
 - behavioral versus anatomical modernity and, 411
 - in Western Asia
 - Amud, 72
 - background regarding, 67
 - conclusions about, 74
 - Dederiyeh Cave, 73–74
 - earliest evidence of, 67, 68t, 69t
 - Kebara 2, 72–73, 73f
 - Mugharet-es-Skhul, 67, 70, 70f
 - Qafzeh, 70–71
 - Shanidar, 71–72, 75n4
 - Tabun C1, 71
- Calvarium, 256, 267, 269, 269f
- CARE. *See* Compound age-specific reproductive energy
- Carpentarians, 125
- Carpometacarpal articulations, 56
- El Castillo Cave, 232
- Center and edge effect, 356–57
- Chaoxian, 98t, 99f, 104
- La Chapelle-aux-Saints, 260t
- Châteauneuf-sur-Charente 1, 259t
- Châtelperronian, 225
 - transitional assemblages,
 - Western Eurasian
 - Arcy-sur-Cure, 227–28, 228f
 - dating of, 227
 - Grotte du Renne, 227–28, 228f, 229
 - overview of, 227
 - Quinçay, 229
 - Saint-Césaire, 228–29
 - Spy, 230
- Chronometric dating techniques, xiii
- Cioclovina
 - cranium, 185–86, 185f
 - dating of, 198
 - modern human remains at, 174t, 176f, 185–87, 185f
 - Neandertal and, 185–87
 - overview about, 174t, 176f, 185
- Cioclovina Cave, 236–37
- Cladistic analysis, 363
- Climate, 24, 295–96
- Combe-Capelle, dating of, 226
- Compound age-specific reproductive energy (CARE), 304
 - daily requirements, 306–7, 306f
 - Neandertal–EUP modern human differences in, 306–7, 307f
 - variable sets contributing to, 305–6
- Continuity with Hybridization Model, 89
 - arguments for, 96
 - Brown and, 95–96
 - criticisms of, 96–97
 - development of, 92–94
 - Etler, and, 95
 - morphological features and, 92–93
 - mosaic evolution and, 93–94
 - mt DNA and, 97
 - Multiregional Evolution compared with, 94
 - other geographical regions and, 93
 - river metaphor and, 95
 - in situ evolution and, 92
 - Wu and, 92–94
- Convergence, 349–50, 382n19
- Cost of transport, 298
- Cranial variation
 - conclusions about, 332–34
 - craniometric distance correlation,
 - with genetic and geographic distance, 330–32, 331f
 - evolution implications, 332–34
 - metric traits and, 332
 - implications for study of, 326–27
 - nature versus nurture and, 327
 - overview about, xviii, 321–22
 - patterns
 - higher phenotypic variation in Africa, 328–29, 328f
 - low levels of phenotypic differentiation, 329
 - phenotypic variation and distance from Africa, 329
 - variation levels in *Homo sapiens*, 327–28

- Craniofacial form, in Western Asia
 Amud and, 61, 61f
 chronological variation and, 62
 Dederiyeh Cave and, 62
 Kebara 2 and, 61–62, 65
 Late Pleistocene, 57–59
 MP, 59–63
 nasal floor and, 64
 overview about, xvii–xviii
 Shanidar and, 60–61
 Skhül-Qafzeh and, 57–59, 58f
 spoken language and, 65
 Tabun C1 and, 62
 Tabun C2 and, 62–63, 63f
 teeth, non-dietary use of, and, 64–65
 Teshik-Tash and, 60
 UP and, 63–64
 Zuttiyeh and, 57, 57f
- Craniofacial growth and development,
 Neandertal
 conclusions, 276–77
 discussion
 issues, 272–74
 life history parameters reconstruction,
 274–75
 postnatal growth, 275–76
 Engis 2 life cycle and, 254f
 materials and methods, study
 aging Neandertals and modern humans,
 261–62
 aging *Pan*, 262
 capturing linear dimensions, 262–63
 euclidean distances calculation, 264–65
 growth trajectories example, 265f
 modeling growth, 263
 modern human sample, 258, 260
 multivariate analysis, 264
 Neandertal sample, 258, 259t
Pan paniscus sample, 260
Pan troglodytes sample, 260
 piecewise regression, 264
 variability within modern human sample,
 263
 overview about, 253–54
 postnatal ontogeny and modern human
 origins, 276–77
 rates of
 accelerated, 255
 calvarium change, 256
 dental development, 255–56
 differences in, 254–56
 mental foramen and, 257
 ontogeny and, 257
 results
 calvarium multivariate analysis, 267, 269,
 269f
 euclidean distances between adults and
 infants, 272, 273f, 273t
 facial dimensions multivariate analysis,
 269–70, 270t, 271f
 mandibular dimensions multivariate
 analysis, 271–72, 271f
 Neandertal and modern human modeled
 growth trajectories, 265, 266t, 267
Pan species modeled growth trajectories,
 267, 268t
 Roc de Marsal life cycle and, 254f
 shape change, 256–57
 similarities in, 256
 Spy 1 life cycle and, 254f
 Craniometric distance correlation, 330–32, 331f
- Cranium
 Africa, evolution of in, 25, 26f
 Australia, Javan ancestry evidence, 131–35
 Cioclovina, 185–86, 185f
 comparisons, 364, 365f
 energetics and, 301
 Kr 1, 166
 Ngaloba, 14
 Oase 2, 183–84, 184f, 192, 198
 Peștera Muierii, 186–87, 186f
 Vindija and, 170, 171f
 Cro-Magnon, dating of, 226
 La Crouzade, 237
 Crvena Stijena tooth, 164, 202n4, 203n8
- Dadong, 99f, 104
 Daily energy expenditure (DEE), 288, 296
 Dali, 98t, 99f, 102, 103f
Homo erectus and, 103
 mosaic of features regarding, 112
 Dame du Cavillon, 203n18
 Danube River valley, 154
 Dar-es-Soltane II, 22–23
 Dederiyeh Cave
 burials, 73–74
 craniofacial form and, 62
 DEE. *See* Daily energy expenditure
 Denisova
 Australia and, 138–39
 bottlenecks and, 340–41
 branching population model and, 342–43
 ILS and, 342
 modern humans sharing genes of, 339
 multiregional admixture and, 360
 West-Central Asia and, 49
 Denisova Cave, genetics and, 193
 Dental issues. *See* Teeth

- Deoxyribonucleic acid. *See*
Mitochondrial DNA
- Devil's Tower 2, 259t
- Devon Downs, 125
- Diet breadth, 299
- Dihybrid Model, 125–26
- Diré Dawa, 21
- DNA. *See* Mitochondrial DNA
- Dolní Věstonice, 175t, 176f, 189–90
- Dzeravá Skála, 172–73, 172t, 232
- Early Upper Paleolithic (EUP),
in Western Eurasia
Assimilation Model and, 224
body mass estimates, 289, 291t
discussion, 237–43
acculturation models, 242
archaic traits, 242–43
Bohunician, 241
burial practices, 238
dental material, 238
environmental changes, 241–42
genetics, 243
Kent's Cavern, 241
remains scarcity, 238
- Early Aurignacian contexts
Bacho Kiro, 232
Brassempouy, 233
Buran Kaya III, 234
Dzeravá Skála, 232
La Ferrassie, 233
Fontana Nuova di Ragusa, 232–33
Fossellone, 232
Kostenki 14, 233–34
Oblazowa, 234
Peștera cu Oase, 234–35, 235f
La Quina-Aval, 233, 233f
- human morphology, overview of, 223
- human remains, geological age revision of,
226–27
- Later Aurignacian contexts
Cioclovina Cave, 236–37
La Crouzade, 237
Görömböly-Tapolca, 237
Istállós-kő, 237
Mladeč, 235–36, 236f
Muierii Cave, 236
Les Rois, 237
- lithic industries found in, 224–25
- main lithic assemblages
chronological distribution of, 240f
geographic distributions of, 239f
- modern human morphology, lineage and,
223–24
- Neandertal–EUP modern human CARE
differences, 306–7, 307f
- Neandertal genetics and, 224
- overview about, xvii, 223–26
- proto-Aurignacian contexts
El Castillo Cave, 232
Isturitz, 231
Le Piage, 231
Riparo Bombrini, 231
- transitional assemblages
Arcy-sur-Cure, 227–28, 228f
Bacho Kiro, 230–31
Châtelperronian, 227–30
dating of, 227
Grotta del Cavallo, 230
Grotte du Renne, 227–28, 228f, 229
overview of, 227
Quinçay, 229
Saint-Césaire, 228–29
Spy, 230
Szeletian, 231
Uluzzian, 230–31
- Ehringsdorf, 156, 157t, 160f
- Eliye Springs, 13
- Enamel development, 301–2
- Energetics
conclusions about, 308
described, 285
energy, reproduction, and evolution
interaction and
energy balance, 287
energy budgets, 286–87, 287f
trade-offs, 287–88
- energy throughput differences and
facial architecture, 304
MET, 302–3
nose size, 303–4
oxygen requirements, 302
respiration rate, 303
respiratory tract and, 303
- history of research in, 285–86
- key concepts, 286–88
- lines of evidence used in, 286
- maintenance
activity energy expenditure, 296–99
BMR and, 288–89, 290t, 291t, 292t, 293,
293t, 294f, 295–96, 295t
body size and energy expenditure, 288–96
DEE and, 288, 296
as energy budget category, 287, 287f
locomotor energetics, 296–99
- nose role and, 405
- overview about, xviii, 285
- Paleobiology and

- Energetics (*cont'd*)
- concerns, 402–4, 401f
 - noses, role of, 405
 - subsistence, 404–5
 - production
 - craniodental and postcranial development and, 301
 - craniofacial traits and, 301
 - enamel development and, 301–2
 - as energy budget category, 287, 287f
 - female energy expenditure and, 300
 - fossil record regarding, 300–302
 - neonate brain growth and, 299–300
 - offspring growth and development, 299–302
 - pelvis and, 300–301
 - somatic maturation and, 300
 - reproduction
 - CARE variable sets, 305–6
 - conclusions about, 308
 - daily CARE requirements, 306–7, 306f
 - energy balance, 287
 - energy budgets, 286–87, 287f
 - fertility rates and, 307–8
 - foraging and, 307
 - model, 305
 - Neandertal–EUP modern human CARE differences, 306–7, 307f
 - overview, 304
 - trade-offs, 287–88
 - researchers in, 285–86
 - study overview, 286
- Energy balance, 287
- Energy budgets, 286–87, 287f
- Energy throughput differences
- facial architecture, 304
 - MET, 302–3
 - nose size, 303–4
 - oxygen requirements, 302
 - respiration and, 303
- Engis 2
- age at death, 259t
 - Neandertal life cycle and, 254f
- Environmental changes, 241–42
- Etler, D. A., 95
- Euclidean distances calculation, 272, 273f, 273t
- EUP. *See* Early Upper Paleolithic, in Western Eurasia
- Eurasia. *See* Early Upper Paleolithic, in Western Eurasia
- Europe
- gracility and, 366f
 - Multiregional Evolution Model, Afro-European sapiens hypothesis and, 382n3
 - Neandertals, body size and shape and, 49–50
- Europe, Central
- conclusions about, 201–2
 - consensus points about, 323
 - Danube River valley and, 154
 - dating and, 152, 153t, 192
 - discussion
 - evidentiary level, 192–93
 - theoretical level, 193–94
 - genetics and, 152, 192–93
 - historical background, 151–56
 - human evolution evidence
 - Aurignacian and, 196–97
 - biological variation, 197–98
 - human appearance and Neandertal disappearance, 198–99
 - MP or UP categories and, 195
 - Neandertal–modern admixture, 199–200, 204nn24–25
 - Neandertal–modern separation, 194–95
 - site-by-site analysis and, 195–96
 - temporal variation, 197
 - transitional industries, 196–97, 203n21
 - transition period regarding, 194–95
 - typology of biology and culture, 194–97, 203n21
 - human fossils, earliest modern
 - La Adam, 174t, 176f, 187
 - Bacho Kiro, 174t, 176f, 187–88
 - Bordu Mare, 174t, 176f, 187
 - Brno-Franzouska, 175t, 176f, 190
 - Cioclovina, 174t, 176f, 185–87, 185f
 - Dolní Věstonice, 175t, 176f, 189–90
 - Görömböly-Tapolca, 174t, 176f, 188
 - Gravettian from Eastern region, 188–92
 - Gravettian from Western region, 178
 - Grub/Kranawetberg, 175t, 176f, 191–92
 - Istállós-kő, 174t, 176f, 178–79, 237
 - limb proportions, 191t
 - locations of, 176f
 - Malu Roșu, 175t, 176f, 187
 - Miesslingtal, 174t, 176f, 178
 - Mladeč, 174t, 176f, 178, 179–82, 182f
 - Oase 1 mandible, 182–83, 183f
 - Oase 2 cranium, 183–84, 184f
 - Oblazowa, 174t, 176f, 188
 - overview about, 173, 174t, 175t, 176f
 - Pavlov, 175t, 176f, 189–90
 - Pavlovian from Eastern region, 188–90, 191t
 - Peștera cu Oase, 175t, 176f, 182–84, 183f, 184f
 - Peștera Mică, 175t, 176f, 187
 - Peștera Muierii, 175t, 176f, 185, 186–87, 186f
 - Předmostí, 175t, 176f, 188–89
 - pre-Gravettian from Eastern region, 178–88

- pre-Gravettian from Western region, 177
 Willendorf I and II, 175t, 176f, 190–91
 Willendorf-Kostienkian from Eastern region, 190–92
 Late Pleistocene, assimilation, 200–201, 204nn26–27
 Neandertal fossils
 dated, 156, 159f
 Dzeravá Skála, 172–73, 172t
 from Eastern region, 164–71, 203n8
 Ehringsdorf, 156, 157t, 160f
 Hohlenstein-Stadel, 157t, 160f, 162–63, 177
 Hunas, 157t, 160f, 163
 of initial UP, 172–73, 172t
 Klausennische, 157t, 160f, 163
 Kleine Feldhofer Grotte, 157t, 159, 160f, 161, 161f
 Krapina, 157t, 160f, 165–67, 167f, 168f
 Mala Balanica, 158t, 160f, 171
 Ochtendung, 157t, 160f, 164
 record overview, 156, 157t, 158t
 Remete Felső, 172, 172t, 173
 Šal'a, 158t, 160f, 164–65
 Sarstedt, 157t, 160f, 162
 Sesselfelsgrötte, 157t, 160f, 163
 sites, 156, 160f
 Stajnia, 158t, 160f, 171
 Suba-lyuk, 158t, 160f, 165
 transitional assemblages and, 172–73, 172t
 Untere Klause, 157t, 160f, 163
 Vindija, 158t, 160f, 168–70, 169f, 171f, 172, 172t, 197, 203nn11–12
 Warendorf-Neuwarendorf, 157t, 160f, 163
 from Western region, 156–64
 Zeeland Ridges, 157t, 160f, 162
 overview about, xvii
 typology of biology and culture
 Aurignacian and, 196–97
 MP or UP categories and, 195
 Neandertal–modern separation, 194–95
 site-by-site analysis and, 195–96
 transitional industries, 196–97, 203n21
 transition period regarding, 194–95
 Velika Pečina and, 178, 203, 226
 Extrasutural bone at lambda, 111
 Eyasi remains, 14

 Feldhofer 1, temporal variation and, 197
 Female
 body mass estimates, compared with male, 289, 290t, 291t, 292t, 293, 293t, 294f
 energy expenditure, 300
 La Ferrassie, 233, 259t
 Fertility rates, 307–8
 Fish Hoek 1, 23

 Florisbad, 12–13
 Fontana Nuova di Ragusa, 232–33
 Foraging
 habits, 296–97
 reproduction and, 307
 Forbes' Quarry, 259t
 Fossellone, 232
Fossil Men (Boule & Vallois), 151
 Founder effects, in Late Pleistocene, 340–41
 Frontal bone, 132–33, 166–67, 167f
 Frontal boss, 111–12

 Gabled vault, 110–11
 Geißenklösterle, 177, 178
 Gene flow, 95, 113, 343
 Genetics
 Australia and, 138–39
 Central Europe and, 152, 192–93
 cranial variation and
 with genetic and geographic distance, 330–32, 331f
 higher phenotypic variation in Africa, 328–29, 328f
 levels in *Homo sapiens*, 327–28
 low levels of phenotypic differentiation, 329
 phenotypic variation and distance from Africa, 329
 Denisova Cave and, 193
 EUP, in Western Eurasia
 discussion, 243
 Neandertal and, 224
 modernity and
 convergence, 349–50
 evolutionary acceleration, 379
 evolutionary stasis, 379
 Neolithic, 377–78
 population acceleration, 378
 timing of, 377
 MSA Africans and, 345–47
 Neandertal contribution regarding, xix–xxi, 193, 199–200, 224
 Neandertal–modern admixture, 199–200
 overview about, 321
 small sample size and, xx–xxi
 variation in living humans
 declines with distance from Africa, 325
 geography and, 326
 higher variation in Africa, 324–25
 low among geographic regions, 325–26
 low levels of, 323–24
 Vindija and, 193
 Weak Garden of Eden Model and, 346
 Western Eurasia and, 243
 what made humans modern and, 349–50

Genomics

- Africa and, xix–xx, 345–47
 - bottlenecks and, 340–41
 - conclusions about, 350–51
 - Denisova, modern humans sharing, 339
 - founder effects and, 340–41
 - ILS and, 342
 - MSA Africans and, 345–47
 - Neandertal, xix–xx
 - modern humans sharing, 339
 - origins clarification via, 339–40
 - overview about, 339–40
 - racial diversity and, 350–51
 - tracers of population history and
 - branching population model, 342–43
 - gene flow, 343
 - HapMap, 343–45, 344f
 - ILS, 342
 - selection, 342–43
 - Weak Garden of Eden Model and, 346
 - what made humans modern
 - amino acid coding sites and, 347–48
 - anatomical similarity and, 347
 - diminishing returns and, 348
 - genetic convergence and, 349–50
 - lactase persistence phenotype and, 348
 - Out-of-Africa Model and, 347
 - skin pigmentation and, 349–50
 - social ecology and technology and, 349
 - Wright-Fisher model and, 340–41
- Gona pelvis, 7–8
- Gorjanović-Kramberger, Dragutin, 151, 165
- Görömböly-Tapolca, 174t, 176f, 188, 237
- Gracile group, 126, 127f
 - bio-culturalist viewpoint regarding, 128, 129
 - migrationist viewpoint regarding, 128–29
 - selectionist viewpoint regarding, 128, 129–30
- Gracility
- Australasia and, 367f
 - Europe and, 366f
 - modernity and, 364–65, 366f, 367f, 368f
- Gravettian
- Cro-Magnon, dating of, 226
 - human fossils, earliest modern
 - from Eastern Central Europe region, 188–92
 - from Western Central Europe region, 178
- Gravettian, pre-, human fossils, earliest modern
 - from Eastern Central Europe region, 178–88
 - from Western Central Europe region, 177
- Grotta del Cavallo, 230
- Grotte du Renne, 227–28, 228f, 229
- Grub/Kranawetberg, 175t, 176f, 191–92
- Guattari 1, 260t

Hähnofersand

- dating of, 177, 192, 226
 - direct dating and, 192
 - incorrect dating and, 177
 - temporal variation and, 197
- Haigh, J., 340–41
- Hand manipulation, 55–56
- HapMap, 343–45, 344f
- Haua Fteah, 23
- Herto, 17–18, 17f
 - modernity and, 365f
- History of Physical Anthropology: An Encyclopedia* (Spencer), xvi
- Hobbit, 139–40
- Hoedjiespunt, 11–12
- Hofmeyr, 20–21
- Hohle Fels, 177, 178
- Hohlenstein-Stadel, 157t, 160f, 162–63
 - Aurignacian Age and, 177
- Homo antecessor*, 8
- Homo erectus*
 - in Africa, 6–8
 - Dadong and, 104
 - Dali and, 103
 - Gona pelvis and, 7–8
 - Homo floresiensis* and, 140
 - KNM-ER 42700 and, 7
 - KNM-OL 45500 and, 7
 - Nanjing and, 100–101
 - recent fossil finds regarding, 6–7
 - Salkhit and, 109
 - Yunxian and, 99–100
- Homo floresiensis*, 139–40
- Homo heidelbergensis*
 - Baringo Kapthurin and, 10–11
 - Berg Aukas and, 11
 - Bodo and, 8–9
 - body mass estimates, 289, 290t
 - Hoedjiespunt and, 11–12
 - Kabwe and, 9–10
 - locomotor energetics and, 298
 - Ndutu and, 10
 - Saldanha and, 9
 - transition to, 8–12
- Homo neanderthalensis*.
See Neandertal
- Honerthöhle, 177
- Hrdlička, Aleš, 151
- Huanglong Cave, 98t, 99f, 109
- Hunas, 157t, 160f, 163
- Hyoid bone, 65
- ILS. See Incomplete lineage sorting
- Incisors, shovel-shaped, 111
- Incomplete lineage sorting (ILS), 342

- Industries
 lithic, 224–25
 transitional, 196–97, 203n21
Istállós-kő, 174t, 176f, 178–79, 237
Isturitz, 231
- Java, Australia ancestry evidence
 concerning
 autapomorphic features and, 134–35
 browridges and, 132
 conclusions about, 135
 cranial features and, 131, 132–35
 cranial vault and, 131
 facial region and, 131
 frontal bone and, 132–33
 nuchal torus and, 133–34
 occipitals and, 134–35
 overview, 130–31
 parietal bones and, 133
Jebel Irhoud remains, 15
 modernity and, 365f
Jebel Sahaba, 65
Jerzmanowician leaf points, 203n21
Jinchuan, 98t, 99f, 109
Jinniushan, 98t, 99f, 101–2, 102f
 mosaic of features and, 112
- Kabwe, 9–10
Kebara 2
 age at death, 259t
 burial, 72–73, 73f
 craniofacial form, 61–62, 65
Keilor
 gene flow and, 113
 modernity and, 365f
 skull, 125, 365f
Kelsterbach
 dating of, 177, 226
 incorrect dating and, 177
Kent's Cavern, 241
Klasies River
 controversies surrounding, 19
 MSA and, 18–19
Klausennische, 157t, 160f, 163
Kleiber equation, 288–89
Kleine Feldhofer Grotte, 157t, 159, 160f, 161, 161f
Kleine Ofnet, 177
KNM-ER 42700, 7
KNM-ES 999, 13–14
KNM-ES 3884, 13
KNM-ES 11693, 13
KNM-OL 45500, 7
Korolevo, 203n21
Kostenki 14, 233–34
Kow Swamp, 126, 127f
 autapomorphic features and, 134
 browridges and, 132
 cranial vault and, 131
 frontal bone and, 132–33
 mandibles and, 131–32
 modernity and, 365f
 nuchal torus and, 133–34
 parietal bones and, 133
Krapina, 157t, 160f
 age of deposits at, 166
 faunal remains at, 203n10
 fragments, age at death and, 259t
 Gorjanović-Kramberger and, 165
 Kr 1 cranium at, 166
 Kr 3 frontal bone at, 166–67, 167f
 Kr 5 occipital bunning at, 167, 168f
 publications on, 165–66
 range of finds at, 165
 temporal variation and, 197
- Lactase persistence phenotype, 348
Laetoli Hominid 18, 14
Lahr, M. M., 96
Laishui, 99f, 108
Lake Mungo, 125–26, 127f
Lambda, extrasutural bone at, 111
Language, 65
Late archaic transitional specimens
 Eliye Springs, 13
 Eyasi remains, 14
 Florisbad, 12–13
 Jebel Irhoud remains, 15
 KNM-ES 999, 13–14
 KNM-ES 3884, 13
 Ngaloba cranium, 14
 Omo II and, 14–15
 overview, 12
Late Stone Age (LSA)
 Dar-es-Soltane II and, 22–23
 Haua Fteah and, 23
 Hofmeyr and, 20–21
 Homo sapiens from Early, 20–23
 Mumbwa and, 21
 Nazlet Khater and, 22
 Porc-épic and, 21
 Taramsa Hill and, 22
Late Upper Paleolithic (LUP), 289, 292t, 293t
Levallois tradition, 203n21
Liang Bua, 139–40
Lieberman, D. E., 96
Limb
 length, 297–98
 proportions, Central European, 191t

- Lithic assemblages, Western Eurasian
 chronological distribution of, 240f
 geographic distributions of, 239f
- Lithic industries, 224–25
- Liujiang, 98t, 99f, 107–8
 gene flow and, 113
 modernity and, 365f
- Locomotion
 landscape use and
 locomotor robusticity, 401–3, 402f
 lower limb abnormalities, 401–3
 in Western Asia, 52–53
- Locomotor energetics
 cost of transport and, 298
 diet breadth and, 299
 efficiency and, 297
 factors influencing, 297
 foraging habits, 296–97
 fossil record and, 297
Homo heidelbergensis and, 298
 issues surrounding, 296
 limb length and, 297–98
 Neandertal and modern human, 298–99
 running and, 299
- Longevity, 373–77, 374f, 375t
- Longlin Cave, 99f, 99t, 108–9
- LSA. *See* Late Stone Age
- Lumpers, 24–25
- LUP. *See* Late Upper Paleolithic
- Maba specimen, 112
- Maintenance, energetics
 activity energy expenditure, 296–99
 BMR and, 288–89, 290t, 291t, 292t, 293, 293t, 294f, 295–96, 295t
 body size and energy expenditure, 288–96
 DEE and, 288, 296
 as energy budget category, 287, 287f
 locomotor energetics, 296–99
- Mala Balanica, 158t, 160f, 171
- Malarnaud, 259t
- Maludong, 99f, 99t, 108–9
- Malu Roşu, 175t, 176f, 187
- Mandible
 Kow Swamp, 131–32
 Oase 1, 182–83, 183f, 192–98
 Peştera Muierii, 187
 Sangiran specimens, 132
- Mandibular dimensions multivariate analysis, 271–72, 271f
- Mandibular torus, 110
- Manipulation
 paleobiology and
 anterior dental attrition, 408, 409f
 archaeological context, 405–7
 summary, 408
 upper limb hypertrophy, 406–8, 407f
 in Western Asia
 carpometacarpal articulations and, 56
 conclusions about, 56
 hand and wrist, 55–56
 upper limb skeleton and, 55
- Maynard Smith, J., 340–41
- Meipu, 115n1
- Mellars, P. A., 382n16
- Mental foramen, 257
- Metabolic equivalent of task (MET), 302–3
- Middle Paleolithic (MP)
 Aurignacian complex and, 225
 behavioral modernity, as demographic process
 and, 373–77, 374f, 375t
 lithic industries and, 224–25
 modern human remains and, 225
 Neandertal remains and, 225
 typology of biology and culture and, 195
 Western Asia, craniofacial form, 59–63
- Middle Stone Age (MSA)
 Africa
 dating in, 2–3
 genetic diversity and, 345–47
 hominins from Late, 20–23
 Dar-es-Soltane II and, 22–23
 dating of, 2–3
 Haua Fteah and, 23
 Hofmeyr and, 20–21
 hominins formerly thought to date to, 23
 Homo sapiens from Late, 20–23
 Klasies River and, 18–19
 Mumbwa and, 21
 Nazlet Khater and, 22
 Porc-épic and, 21
 Taramsa Hill and, 22
 Weak Garden of Eden Model and, 346
- Miesslingtal, 174t, 176f, 178
- Migration
 Australian multiple, 128–30
 bio-culturalist viewpoint, 128, 129
 migrationist viewpoint, 128–29
 selectionist viewpoint, 128, 129–30
 out of Africa, xv–xvi
- Mitochondrial (mt) DNA, xiii
 Africa and, 1–2
 Multiregional Evolution Model and, 96
- Mixed ancestry, 360, 361f
- Mladeč, 178
 artifacts from, 180
 craniodental remains from, 180–81
 dating and, 179–80, 192, 198, 203nn15–16

- direct dating and, 192
- Later Aurignacian and, 235–36, 236f
- Neandertal contribution regarding, 181
- occipital bunning and, 181
- overview of, 174t, 176f, 179
- postcranial remains from, 180
- suprainiac fossa and, 181–82, 182f
- Models. *See specific model*
- Modernity
 - adaptive introgression and, 360, 382n10
 - anatomical
 - African anatomy and, 363–65, 365f
 - Assimilation Model and, 364
 - cladistic analysis and, 363
 - cranium comparisons and, 364, 365f
 - early, 365, 367–69
 - gracility and, 364–65, 366f, 367f, 368f
 - mixture involved in, 369
 - no single source of, 363
 - overview, 363
 - problematic areas regarding, 363
 - behavioral
 - archaeological evidence, 370–71
 - cone of, 372
 - as demographic process, 373–77, 374f, 375t
 - human revolution and, 371–73
 - longevity and, 373–77, 374f, 375t
 - Mellars and, 382n16
 - oral traditions and, 375–76
 - positive feedback and, 375
 - process focus regarding, 371–72
 - questions surrounding, 370
 - repetition and, 376
 - resources transfer and, 375–76
 - Wobst and, 372
 - behavioral versus anatomical
 - art, geometric and representational, 414
 - body decoration, 413–15
 - burials, 413
 - implications, 414–16
 - overview, 412
 - technology, 412–14
 - conclusions about, 380–81
 - definitions surrounding, 359
 - East Asia and, 113–14
 - genetic
 - convergence, 349–50
 - evolutionary acceleration and, 379
 - evolutionary stasis and, 379
 - Neolithic and, 377–78
 - population acceleration and, 378
 - timing of, 377
 - mixed ancestry and, 360, 361f, 382nn12–13
 - multiregional admixture and, 360
 - Multiregional Evolution Model and, 358–59
 - Neandertals are us and, 362
 - as process, 362
 - single unique ancestry and, 359
 - timing of, 358–59
 - Weidenreich's polycentric model and, 360, 382n12
- Monte Circeo II, 260t
- Monte Circeo III, 259t
- Mosaic, 112
 - evolution, 93–94
- MP. *See* Middle Paleolithic
- MSA. *See* Middle Stone Age
- mt DNA. *See* Mitochondrial DNA
- Mugharet-es-Skhul, 67, 70, 70f
- Muierii, 198. *See also* Peștera Muierii
- Muierii Cave, 236
- Multiregional admixture, 360
- Multiregional Evolution Model, 89–90
 - Afro-European sapiens hypothesis and, 382n3
 - arguments for, 96
 - center and edge effect and, 356–57
 - classes of, 356, 382n3
 - Continuity with Hybridization Model
 - compared with, 94
 - criticisms of, 96–97
 - gene flow and, 95
 - history surrounding, xii–xiv
 - human evolution and, 356–58
 - key insight of, 358
 - middle ground regarding, 193–94
 - mischaracterization of, 94
 - modernity issues and, 358–59
 - morphological continuity of fossils and, 94–95
 - mt DNA and, 97
 - other species and, 381n1
 - overview about, 356
 - Pope and, 95
 - principles of, 94
 - river metaphor and, 95
 - Thorne and, 94–95, 124
 - Trinkaus and, 193
 - variation by region and time and, 357–58, 357f, 382n5
 - Wolpoff and, 94–95
 - Wu and, 94–95
- Multivariate analysis, 264
 - calvarium, 267, 269, 269f
 - facial dimensions, 269–70, 270t, 271f
 - mandibular dimensions, 271–72, 271f
- Mumbwa, 21
- Münzel, 177
- Murray Black collection, 123
- Murrayians, 125

- Nanjing, 99f, 100–101, 101f
 Narmada skull, 112
 Nasal floor, 64
 Nature versus nurture, 327
 La Naulette, 259t
 Nazlet Khater, 22
 Ndutu, 10
 Neandertal
 activity energy expenditure and, 298–99
 amino acid coding sites and, 347–48
 BMR and, 289, 290t
 body size and shape, 49–50
 bottlenecks and, 340–41
 branching population model and, 342–43
 Central European fossils
 dated, 156, 159f
 Dzeravá Skála, 172–73, 172t
 from Eastern region, 164–71, 203n8
 Ehringsdorf, 156, 157t, 160f
 Hohlenstein-Stadel, 157t, 160f, 162–63, 177
 Hunas, 157t, 160f, 163
 Klausennische, 157t, 160f, 163
 Kleine Feldhofer Grotte, 157t, 159, 160f, 161, 161f
 Krapina, 157t, 160f, 165–67, 167f, 168f
 Mala Balanica, 158t, 160f, 171
 Mladeč and, 174t, 176f, 178, 179–82, 182f
 Ochtendung, 157t, 160f, 164
 record overview, 156, 157t, 158t
 Remete Felső, 172, 172t, 173
 Šal'a, 158t, 160f, 164–65
 Sarstedt, 157t, 160f, 162
 Sesselfelsgrötte, 157t, 160f, 163
 sites, 156, 160f
 Stajnia, 158t, 160f, 171
 Suba-lyuk, 158t, 160f, 165
 Untere Klause, 157t, 160f, 163
 Vindija, 158t, 160f, 168–70, 169f, 171f, 172, 172t, 179, 203nn11–12
 Warendorf-Neuwarendorf, 157t, 160f, 163
 from Western region, 156–64
 Zeeland Ridges, 157t, 160f, 162
 Central Europe human evolution evidence
 biological variation, 197–98
 human appearance and Neandertal disappearance, 198–99
 Neandertal–modern admixture, 199–200, 204nn24–25
 Neandertal–modern separation, 194–95
 temporal variation, 197
 typology of biology and culture, 194–97
 Chaoxian and, 104
 Cioclovina and, 185–87
 consensus points about, 323
 craniofacial form
 Amud and, 61, 61f
 chronological variation and, 62
 Dederiyeh Cave and, 62
 Kebara 2 and, 61–62, 65
 Late Pleistocene, 57–59
 MP, 59–63
 nasal floor and, 64
 overview about, xvii–xviii
 Shanidar and, 60–61
 Skhul-Qafzeh and, 57–59, 58f
 spoken language and, 65
 Tabun C1 and, 62
 Tabun C2 and, 62–63, 63f
 teeth, non-dietary use of, and, 64–65
 Teshik-Tash and, 60
 UP and, 63–64
 Zuttiyeh and, 57, 57f
 genetics and, xix–xxi, 193
 Neandertal–modern admixture, 199–200
 Western Eurasia, 224
 genomics, xix–xx
 modern humans sharing, 339
 ILS and, 342
 Liujiang and, 107–8
 locomotor energetics, 298–99
 longevity and, 373–77, 374f, 375t
 Maba specimen and, 112
 mixed ancestry and, 360, 361f
 mixture and, 369
 modern humans sharing genes of, 339
 multiregional admixture and, 360
 Oase 1 mandible and, 183
 Oase 2 cranium and, 183–84, 184f
 reproduction energetics
 CARE variable sets, 305–6
 conclusions about, 308
 daily CARE requirements, 306–7, 306f
 fertility rates and, 307–8
 foraging and, 307
 model, 305
 Neandertal–EUP modern human CARE differences, 306–7, 307f
 overview, 304
 Salkhit and, 109
 thoracic morphology, 51–52
 Tianyuan Cave and, 107
 tracers of population history and, 342–45, 344f
 Trinkaus and, 204n24
 as us, 362
 West-Central Asia and, 48–49
 Western Asia
 Amud and, 61, 61f
 birthing and, 53–55
 carpometacarpal articulations and, 56

- Dederiyeh Cave and, 62
- European Neandertal and, 49–50
- hand and wrist and, 55–56
- Kebara 2 and, 61–62, 65
- Late Pleistocene, 46–48
- locomotion, 52–53
- MP, 59–63
- nasal floor and, 64
- Shanidar and, 60–61, 66–67
- Skhul-Qafzeh and, 57–59, 58f
- spoken language and, 65
- Tabun C1 and, 62
- Tabun C2 and, 62–63, 63f
- TEE and, 52
- teeth, non-dietary use of, and, 64–65
- Teshik-Tash and, 60
- thoracic morphology, 51–52
- upper limb skeleton and, 55
- Zuttiyeh and, 57, 57f
- Western Eurasia
 - Châtelperronian, 225
 - genetics and, 224
 - MP and, 225
 - Uluzzian, 226
- Western Eurasian transitional assemblages
 - Arcy-sur-Cure, 227–28, 228f
 - at Bacho Kiro, 231
 - Châtelperronian, 227–30
 - dating of, 227
 - Grotte du Renne, 227–28, 228f, 229
 - overview of, 227
 - Quinçay, 229
 - Saint-Césaire, 228–29
 - Spy, 230
- Neandertal, craniofacial growth and development
 - conclusions, 276–77
 - discussion
 - issues, 272–74
 - life history parameters reconstruction, 274–75
 - postnatal growth, 275–76
 - Engis 2 life cycle and, 254f
 - materials and methods
 - aging Neandertals and modern humans, 261–62
 - aging *Pan*, 262
 - capturing linear dimensions, 262–63
 - euclidean distances calculation, 264–65
 - growth trajectories example, 265f
 - modeling growth, 263
 - modern human sample, 258, 260
 - multivariate analysis, 264
 - Neandertal sample, 258, 259t
 - Pan paniscus* sample, 260
 - Pan troglodytes* sample, 260
 - piecewise regression, 264
 - variability within modern human sample, 263
 - overview about, 253–54
 - postnatal ontogeny and modern human origins, 276–77
 - rates of
 - accelerated, 255
 - calvarium change, 256
 - dental development, 255–56
 - differences in, 254–56
 - mental foramen and, 257
 - ontogeny and, 257
 - results
 - calvarium multivariate analysis, 267, 269, 269f
 - euclidean distances between adults and infants, 272, 273f, 273t
 - facial dimensions multivariate analysis, 269–70, 270t, 271f
 - mandibular dimensions multivariate analysis, 271–72, 271f
 - Neandertal and modern human modeled growth trajectories, 265, 266t, 267
 - Pan* species modeled growth trajectories, 267, 268t
 - Roc de Marsal life cycle and, 254f
 - shape change, 256–57
 - similarities in, 256
 - Spy 1 life cycle and, 254f
- Negritos, 124
- Neolithic, genetic modernity and, 377–78
- Neonate brain growth, 299–300
- Ngaloba cranium, 14
- Ngandong
 - autapomorphic features and, 134–35
 - browridges and, 132
 - frontal bone and, 133
 - nuchal torus and, 133–34
 - parietal bones and, 133
- Niah, gene flow and, 113
- Niah Cave skull, 125, 126
- Nose
 - pinched, 110
 - role of, human energetic issues and, 405
 - size, energy throughput
 - differences and, 303–4
- Nuchal torus, 133–34
- Oase 1 mandible, 182–83, 183f
 - direct dating and, 192, 198
- Oase 2 cranium, 183–84, 184f
 - direct dating and, 192, 198
- Oblazowa, 174t, 176f, 188, 234

- Occipital
 bunning, 167, 168f, 181
 Javan ancestry evidence and, 135
- Ochoz, 259t
- Ochtendung, 157t, 160f, 164
- Okladnikov Cave, 49
- Omo I, 15–16
- Omo II, 14–16
- Omo-Kibish, xiv
- Ontogeny, 257, 276–77
- Oral traditions, 375–76
- The Origins of Modern Humans: A World Survey of the Fossil Evidence* (Smith & Spencer), xi
 overview of, xii
- Out-of-Africa Model
 middle ground regarding, 193–94
 recent, 89–90
 Trinkaus and, 193
 what made humans modern and, 347
- Oxygen requirements, 302
- Paderborn-Sande
 direct dating and, 192
 incorrect dating and, 177
- PAL. *See* Physical activity level
- Paleoanthropology
 consensus points, 322–23
 model development in, xii–xvi, 89–90
 model falsification criteria, xii–xiii
 in 1984, xii
- Paleobiology
 background concerning, 393–94
 behavioral versus anatomical modernity
 art, geometric and representational, 418
 body decoration, 413–14
 burials, 413
 implications, 414–15
 overview, 412
 technology, 412–13
 discussion, 417–18
 human energetic issues
 concerns, 402–4, 403f
 noses, role of, 405
 subsistence, 404–5
 implications of paleobiological complexes
 behavioral versus anatomical modernity, 412–15
 human energetic issues, 402–5, 403f
 life history issues, 415–17, 416f
 locomotion and landscape use, 400–2
 manipulation, 405–8, 407f, 409f
 populational issues, 399–400
 samples of concern, 398–99
 stress and survival, 408–12, 410f
 life history issues
 developmental rates, 415–16
 mortality patterns, 416–17, 416f
 overview, 415
 summary, 417
 locomotion and landscape use
 locomotor robusticity, 400–1, 402f
 lower limb abnormalities, 401–2
 manipulation
 anterior dental attrition, 408, 409f
 archaeological context, 405–7
 summary, 408
 upper limb hypertrophy, 406–8, 407f
 overview about, xviii
 stress and survival
 abnormalities, serious, 411–12, 4011f
 archaeological correlations, 398
 dento-alveolar lesions, 412
 developmental stress indications, 409–10
 1990s–2000s perspective, 397–98
 overview, 408–9
 trauma, 410–11
 Twentieth Century perspective
 chronology, 395–96
 early modern human paleobiology, 397
 functional anatomical shifts, 396–97
 1970s–1980s, 394–95
 1990s–2000s, 395–98
 population processes, 395
 stress and survival, 397–98
- Paleolithic. *See* Early Upper Paleolithic; Late Upper Paleolithic; Middle Paleolithic; Upper Paleolithic
- Pan*
 aging, 262
 Pan paniscus sample, 260
 Pan troglodytes sample, 260
 species modeled growth trajectories, 267, 268t
- Parietal bones, 133
- Pavlov, 175t, 176f, 189–90
- Pavlovian, from Eastern region, 188–90, 191t
- Pech de l'Azé, 259t
- Peking Man. *See* *Sinanthropus pekinensis*
- Pelvis
 energetics and, 300–301
 Gona, 7–8
 Tabun C1, 54–55
- Peștera cu Oase, 175t, 176f, 234–35, 235f
 Oase 1 mandible at, 182–83, 183f
 Oase 2 cranium at, 183–84, 184f
 overview about, 182
- Peștera Mică, 175t, 176f, 187

- Peștera Muierii
 cranium, 186–87, 186f
 mandible, 187
 modern human remains at, 175t, 176f, 185, 186–87, 186f
 overview about, 175t, 176f, 185
- Phylogeny, human
 background, 355–56
 contentious nature of, 355
 modernity as process and, 362
 Rightmire's, 3f
 Stringer's, 27f
- Physical activity level (PAL), 296
- Le Pige, 231
- Piecewise regression, 264
- Pinched nose, 110
- Pleistocene, Late
 bottlenecks in, 340–41
 Central Europe, assimilation, 200–201, 204nn26–27
 founder effects in, 340–41
 social ecology and technology and, 349
 Western Asia
 anatomical and taxonomic variability, 46–48
 craniofacial form and, 57–59
- Pleistocene, Middle, 48
- Pope, G. G., 95
- Porc-épic, 21
- Positive feedback, 375
- Postnatal
 growth, 275–76
 ontogeny and modern human origins, 276–77
- Předmostí, 175t, 176f, 188–89
- Production, energetics
 craniodental and postcranial development and, 301
 craniofacial traits and, 301
 enamel development and, 301–2
 as energy budget category, 287, 287f
 female energy expenditure and, 300
 fossil record regarding, 300–302
 neonate brain growth and, 299–300
 offspring growth and development, 299–302
 pelvis and, 300–301
 somatic maturation and, 300
- Qafzeh, 70–71. *See also* Skhul-Qafzeh
- La Quina, 259t
- La Quina-Aval, 233, 233f
- Quinçay, 229
- Quyuan River Mouth, 98t, 99–100, 99f
- origins of, xiii
 verification of, xiv–xv
- Recent Out of Africa Model, 89–90
- Regional continuity
 in Australasia, 367f
 in Europe, 366f
- Regionally predominant features, 381n2
- Remete Cave, 231
- Remete Felső, 172, 172t, 173
- Replacement models, 124
- Reproduction, energetics
 CARE variable sets, 305–6
 conclusions about, 308
 daily CARE requirements, 306–7, 306f
 energy balance, 287
 energy budgets, 286–87, 287f
 fertility rates and, 307–8
 foraging and, 307
 model, 305
 Neandertal–EUP modern human CARE differences, 306–7, 307f
 overview, 304
 trade-offs, 287–88
- Resources transfer, 375–76
- Respiration, 303
- Revolution, human, 371–73
- Rightmire's phylogeny, 3f
- Riparo Bombrini, 231
- River metaphor, 95
- Robust group, 126, 127f
 bio-culturalist viewpoint regarding, 128, 129
 migrationist viewpoint regarding, 128–29
 selectionist viewpoint regarding, 128, 129–30
- Roc de Marsal
 age at death, 259t
 Neandertal life cycle and, 254f
- Les Rois, 237
- Rotational birthing, 53–54
- Running, 299
- Saint-Césaire, 228–29
- Šal'a, 158t, 160f, 164–65
 temporal variation and, 197
- Saldanha, 9
- Salkhit, 99f, 99t, 109
- Sambungmacan, 135
- Sangiran specimens
 cranial vault and, 131
 facial region and, 131
 mandibles and, 132
 nuchal torus and, 133
- Sarstedt, 157t, 160f, 162
- Schafstall, 177

- Schmalzer, S., 92
 Schwalbe, Gustav, 151
 Sclayn, 259t
 Selectionist viewpoint, 128, 129–30
 Sesselfelsgrötte, 157t, 160f, 163
 Shanidar
 burials and, 71–72, 75n5
 craniofacial form and, 60–61
 trauma and, 66–67
 Shovel-shaped incisors, 111
Sinanthropus pekinensis, 90–92
 Singa, 18
 Single Population Model, 128
 Single unique ancestry, 359
 Šipka, 259t
 Sirgenstein, 177
 Skhül 2, 368, 368f
 Skhül 5, 67, 70, 70f
 Skhül Cave, 66
 Skhül-Qafzeh
 body mass estimates, 289, 291t
 samples
 carpometacarpal articulations and, 56
 craniofacial form and, 57–59, 58f
 hand and wrist and, 55–56
 locomotion and, 52–53
 stature and, 50–51
 trauma and, 66
 upper limb skeleton and, 55
 Skin pigmentation, 349–50
 Smith, Fred H., xi
 Social ecology and technology, 349
 Somatic maturation, 300
 Speciation
 Africa and, 24–26, 26f, 27f
 lumpers and, 24–25
 multiregional view of, 25
 splitters and, 24
 Spencer, Frank, xi, xvi–xvii
 Speth, J. D., 382n17
 Splitters, 24
 Spy, 230
 Spy 1
 age at death, 259t
 Neandertal life cycle and, 254f
 Spy 2, 259t
 Stajnia, 158t, 160f, 171
 Stature, 50–51
 Stone Age. *See* Late Stone Age; Middle Stone Age
 St. Prokop 1, 226
 Streletsian leaf points, 203n21
 Stress and survival, paleobiology and
 abnormalities, serious, 4011–12, 411f
 archaeological correlations, 398
 dento-alveolar lesions, 412
 developmental stress indications, 409–10
 1990s–2000s perspective, 397–98
 overview, 408–9
 trauma, 410–11
 Stringer, C. B., 27f, 96
 Stringer's phylogeny, 27f
 Suba-lyuk, 158t, 160f, 165
 Suba-lyuk 2, 259t
 Survival, paleobiology
 abnormalities, serious, 411–12, 410f
 archaeological correlations, 398
 dento-alveolar lesions, 412
 developmental stress indications, 409–10
 1990s–2000s perspective, 397–98
 overview, 408–9
 trauma, 410–11
 Svatý Prokop, 178
 Swabian Jura, 177
 Szeletian, 231
 leaf points, 203n21
 Tabun
 C1, 47, 259t
 burials and, 71
 craniofacial form, 62
 pelvis, 54–55
 C2, craniofacial form, 62–63, 63f
 Taramsa Hill, 22
 TEE. *See* Total energy expenditure
 Teeth
 anterior dental attrition, 408, 409f
 Aurignacian period and, 238
 craniodental and postcranial development
 and, 301
 Crvena Stijena, 164, 202n4, 203n8
 enamel development, 301–2
 Mladeč craniodental remains, 180–81
 non-dietary use of, 64–65
 rates of development, 255–56
 Temnata Cave, 203n21
 Teshik-Tash, 60
 Teshik-Tash 1, 48–49
 age at death, 259t
 Thorne, A. G., 94–95
 Dihybrid Model of, 125–26
 overview about, 124
 Tianyuan Cave, 98t, 99f, 105, 106f, 107
 mosaic of features regarding, 112
 Total energy expenditure (TEE), 52
 Trade-offs, 287–88
 Transitional assemblages, Western Eurasian
 Châtelperronian

- Arcy-sur-Cure, 227–28, 228f
- dating of, 227
- Grotte du Renne, 227–28, 228f, 229
- overview of, 227
- Quinçay, 229
- Saint-Césaire, 228–29
- Spy, 230
- overview of, 227
- Szeletian, 231
- Uluzzian, 230–31
 - Bacho Kiro, 230–31
 - Grotta del Cavallo, 230
- Transitional industries, 196–97, 203n21
- Transport, cost of, 298
- Trauma
 - paleobiology and, stress and survival, 410–11
 - in Western Asia
 - Jebel Sahaba and, 65
 - Shanidar and, 66–67
 - Skhül Cave and, 66
- Trihybrid Model, 124–25
- Trinkaus, E., 193, 204n24
- Tuinplaas, 23
- Typology of biology and culture, Central Europe and
 - Aurignacian and, 196–97
 - MP or UP categories and, 195
 - Neandertal–modern separation, 194–95
 - site-by-site analysis and, 195–96
 - transitional industries, 196–97, 203n21
 - transition period regarding, 194–95
- Uluzzian, 196, 226
 - transitional assemblages, Western Eurasian
 - Bacho Kiro, 230–31
 - Grotta del Cavallo, 230
- Untere Klause, 157t, 160f, 163
- UP. *See* Upper Paleolithic
- Upper limb
 - hypertrophy, 406–8, 407f
 - skeleton manipulation, 55
- Upper Paleolithic (UP)
 - behavioral modernity, as demographic process and, 373–77, 374f, 375t
 - Neandertal fossils and, 172–73, 172t
 - typology of biology and culture and, 195
 - Western Asia, craniofacial form, 63–64
 - cranial specimen from, 170, 171f
 - direct dating and, 192
 - genetics and, 193
 - morphological intermediacy of, 170
 - overview about, 168
 - stratigraphic complexes of, 168, 203nn11–12
 - temporal variation and, 197
 - transitional assemblages and, 172, 172t
- Vogelherd
 - Aurignacian Age and, 177
 - dating of, 177, 192, 226
 - direct dating and, 192
 - incorrect dating and, 177
- Wadjak, 113
- Wajak 1 skull, 125, 126
- Warendorf-Neuwarendorf, 157t, 160f, 163
- Weak Garden of Eden Model, 346
- Weidenreich, Franz, 360, 382n12
 - Australian forms and, 126
 - misinterpretations regarding, 91
 - Sinanthropus pekinensis* and, 90–92
- Weidenreich's polycentric model, 91–92, 360, 382n12
- West-Central Asia, 48–49
- Western Eurasia
 - Assimilation Model and, 224
 - consensus points about, 323
 - discussion, 237–43
 - acculturation models, 242
 - archaic traits, 242–43
 - Bohunician, 241
 - burial practices, 238
 - dental material, 238
 - environmental changes, 241–42
 - genetics, 243
 - Kent's Cavern, 241
 - remains scarcity, 238
- Early Aurignacian contexts
 - Bacho Kiro, 232
 - Brassempouy, 233
 - Buran Kaya III, 234
 - Dzeravá Skála, 232
 - La Ferrassie, 233
 - Fontana Nuova di Ragusa, 232–33
 - Fossellone, 232
 - Kostenki 14, 233–34
 - Oblazowa, 234
 - Peștera cu Oase, 234–35, 235f
 - La Quina-Aval, 233, 233f
- EUP human remains, geological age
 - revision of, 226–27
- human morphology, overview of, 223
- Later Aurignacian contexts
- Vallois, H. V., 151
- Velika Pećina, 178, 203
 - dating of, 226
- Vindija, 158t, 160f, 179
 - biology interpretations of, 170
 - chronology of fossils at, 168–70, 169f

Western Eurasia (*cont'd*)

- Cioclovina Cave, 236–37
- La Crouzade, 237
- Görömböly-Tapolca, 237
- Istállós-kő, 237
- Mladeč, 235–36, 236f
- Muierii Cave, 236
- Les Rois, 237
- lithic industries found in, 224–25
- main lithic assemblages
 - chronological distribution of, 240f
 - geographic distributions of, 239f
- modern human morphology, lineage and, 223–24
- Neandertal genetics and, 224
- overview about, xvii, 223–26
- proto-Aurignacian contexts
 - El Castillo Cave, 232
 - Isturitz, 231
 - Le Piage, 231
 - Riparo Bombrini, 231
- transitional assemblages
 - Arcy-sur-Cure, 227–28, 228f
 - Bacho Kiro, 230–31
 - Châtelperronian, 227–30
 - dating of, 227
 - Grotta del Cavallo, 230
 - Grotte du Renne, 227–28, 228f, 229
 - overview of, 227
 - Quinçay, 229
 - Saint-Césaire, 228–29
 - Spy, 230
 - Szeletian, 231
 - Uluzzian, 230–31

- Willandra Lakes Hominid 50 (WLH), 136f
 - conclusions about, 138
 - controversies surrounding, 135–36
 - dating of, 137–38
 - frontal bone and, 133
 - pathology of, 137
- Willendorf I and II, 175t, 176f, 190–91
- Willendorf-Kostienkian, 190–92
- WLH. *See* Willandra Lakes Hominid 50
- Wobst, H. M., 372
- Wolpoff, M. H., 94–95, 96, 126
- Wright-Fisher model, 340–41
- Wrist manipulation, 55–56
- Wu, X. Z.
 - Continuity with Hybridization Model and, 92–94
 - mosaic evolution and, 93–94
 - Multiregional Evolution Model and, 94–95
 - river metaphor of, 95
- Xichun, 115n1
- Xinglong, 115n1
- Y chromosomes, 2
- Yunxian, 98t, 99–100, 99f
- Zeeland Ridges, 157t, 160f, 162
- Zhirendong, 98t, 99f, 104–5, 105f
 - mosaic of features regarding, 112
- Zhoukoudian region, 90–92
- Zlatý Kůn, 178
 - dating of, 226
- Zuttiyeh, 57, 57f

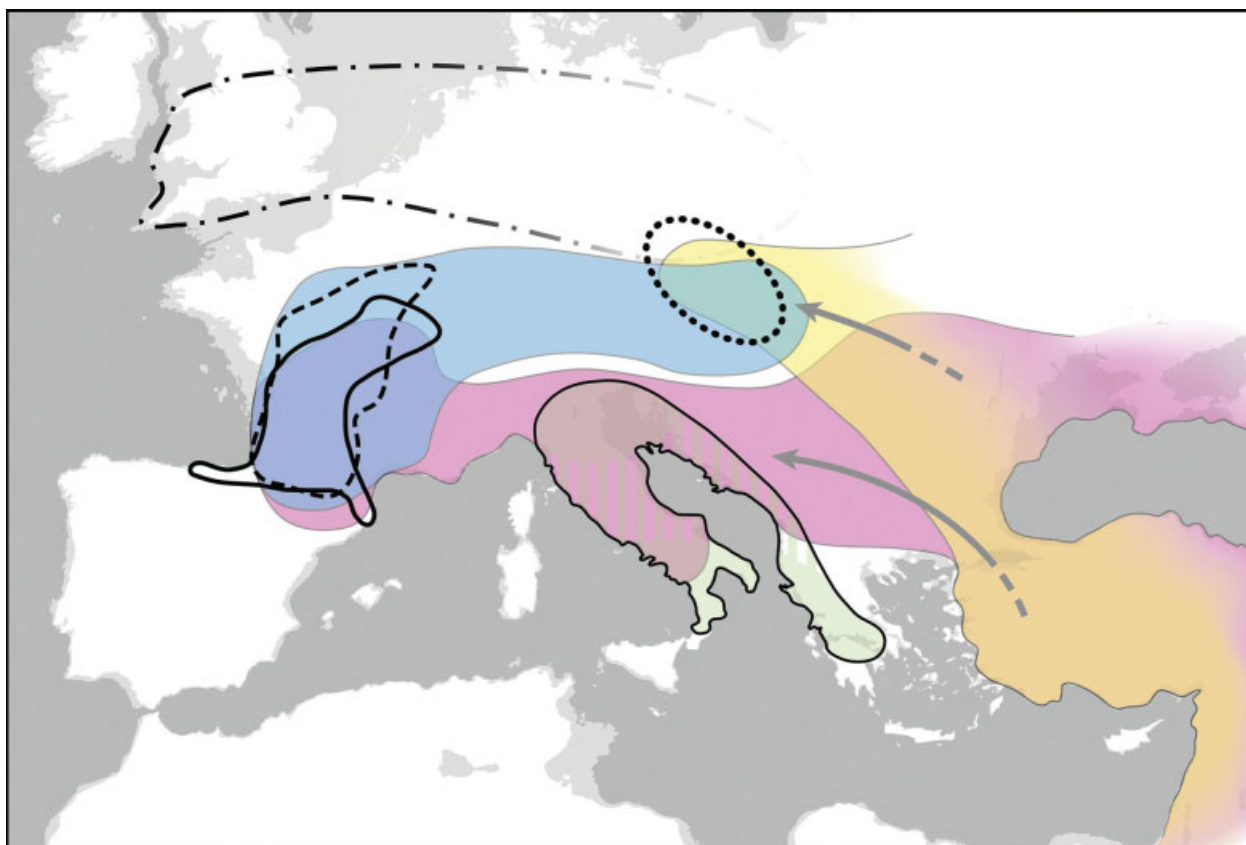


Figure 6.5. Geographical distributions of the main lithic assemblages of western Eurasia between 50 and 35 ka cal BP. With the exception of the MTA, the late Mousterians are not represented. Colored areas represent assemblages tentatively assigned to modern humans and areas limited by thick black lines are tentatively assigned to late Neandertals. ■ Emirian/Bachokirian/Bohunician, ■ Early Ahmarian/Kozarnikian/Protoaurignacian, ■ Early Aurignacian, ■ Uluzzian, Szeletian, ---- MTA, — Châtelperronian, — . — LRJ.

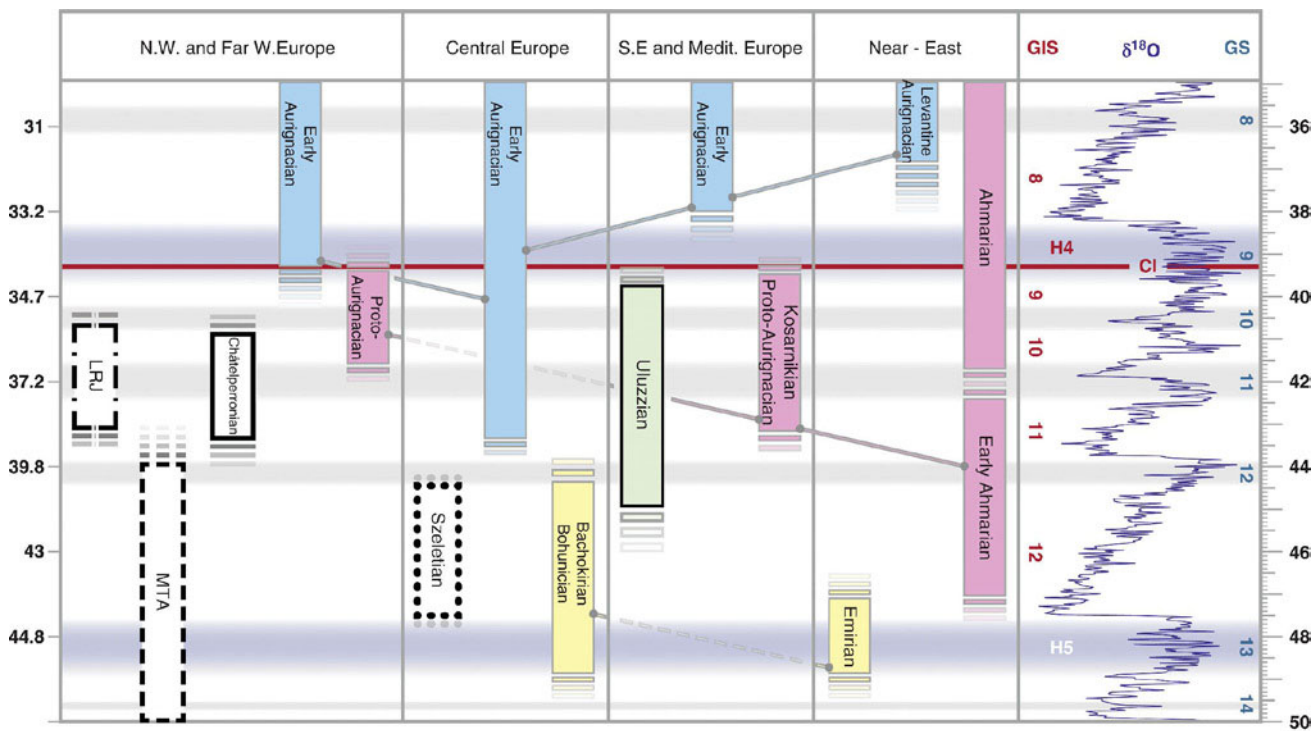


Figure 6.6. Tentative chronological distribution of the assemblages listed in Figure 6.5. The timescale on the right side is calibrated and the timescale on the left side provides an approximate equivalent in ^{14}C chronology (Bronk Ramsey, 2009; Reimer et al., 2009). The curve of the $\delta^{18}\text{O}$ variations in the North Greenland Ice-Core Project (NGRIP) is from <http://www.gfz.ku.dk/~www-glac/data/gripdelta.dat>. Gray horizontal bands indicate cold stadials (GS), and the white horizontal bands indicate the interstadial periods (GIS). Heinrich Events 4 (H4) and 5 (H5) are indicated in blue and the time of the mega-eruption of the Campanian Ignimbrite (CI) is indicated by a red line.